The potential of migratory birds to adapt to global change: lessons from European long-distance migrants and Iberian Blackcaps

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El potencial de las aves para adaptarse al cambio climático: lecciones de las aves europeas migratorias de larga distancia y de las Currucas Capirotadas (*Sylvia atricapilla*) ibéricas

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Memoria presentada por el licenciado Michelangelo Morganti para optar al grado de Doctor en Ciencias Biológicas, bajo la dirección de los Doctores Francisco Pulido Delgado de la Universidad Complutense de Madrid y del Doctor Oscar Gordo Villoslada de la Estación Experimental de Zonas Áridas del Consejo Superior de Investigaciones Científicas.

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a Olmo. meraviglioso frutto

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“ It is not the strongest of the species that survives,

nor the most intelligent that survives.

It is the one that is the most adaptable to change. ”

Charles Darwin, 1859

Abstract

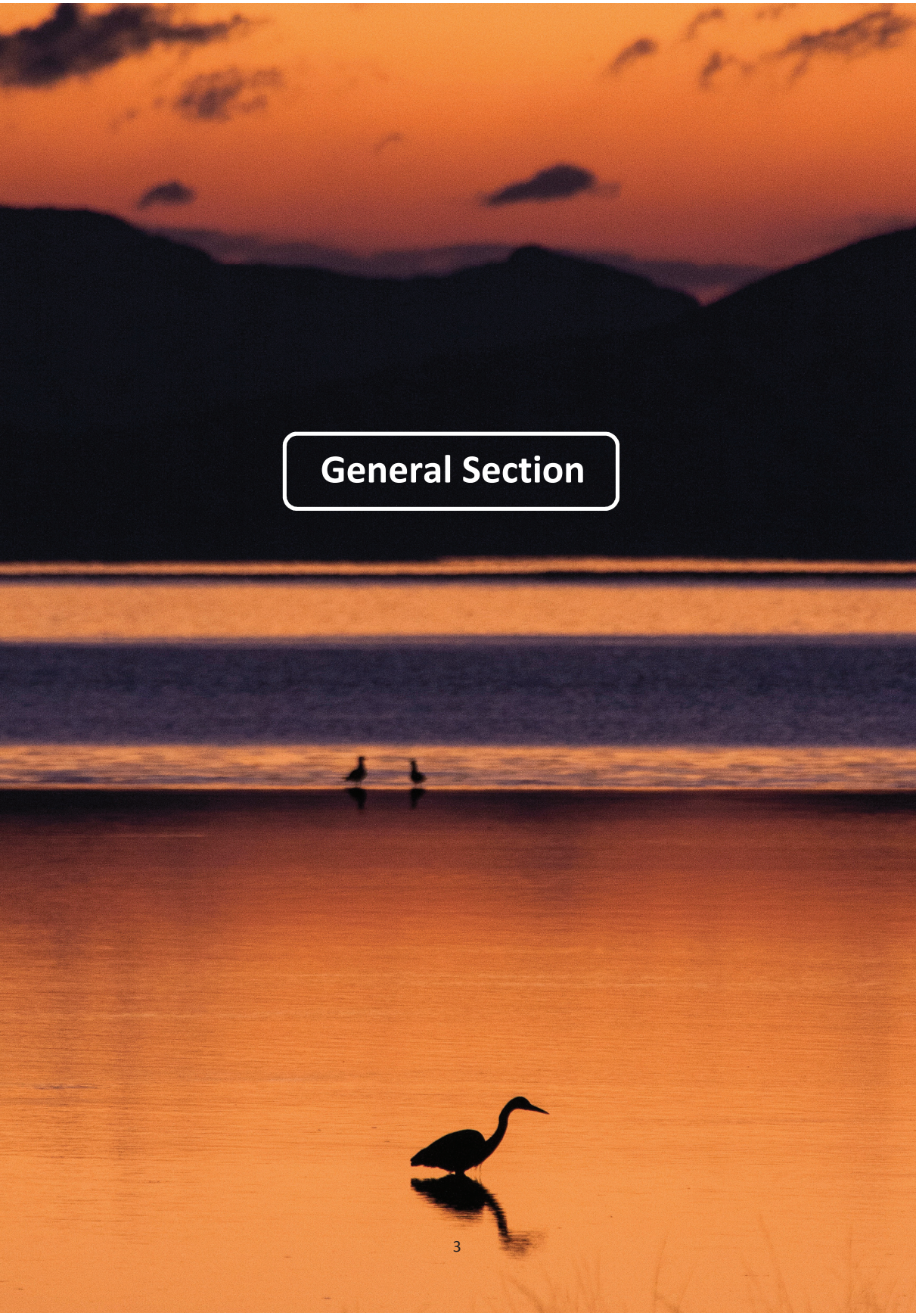
Recent climate change is altering the migratory behaviour of many bird species. An advancement in the timing of spring events and a shift in the geographical distribution have been detected for birds around the world. In particular, intra-Palearctic migratory birds have advanced arrivals in spring and shortened migratory distances by shifting northward their wintering grounds. These changes in migration are considered adaptive responses facilitating the adjustment of the life-cycle to the phenological changes found in their areas of reproduction. Long-distance migrants and short-distance migrants breeding in the same regions are exposed to the same selective pressures. Yet, while the shortening of migration is well established in short-distance migrants, hitherto no research has systematically studied the potential for shortening migration distance in long-distance migrants. Adaptive capacity is expected to differ between species differing in the control of migratory behaviour, according to the evidences that suggest the inability of long-distance migrant passerines to undertake adaptive changes. Studies on a population scale could be key to assess the adaptive potential of migratory birds by identifying the factors that contribute to the adjustment of the phenotype to environmental changes.

The main aim of this thesis is to give new insights on the capacity of migratory birds to adapt to global change. This goal has been pursued at two different spatial and temporal scales, following a top-to-bottom approach. The first part of the thesis is dedicated to explore patterns and potential causes of the recent shortening of migration distance in trans-Saharan migrants along the Western European flyway. This section is based on the data gathered by the compilation of all published winter observations in the Iberian Peninsula and Morocco of 80 species of European trans-Saharan birds between 1969 and 2006. Since adaptive processes happen at the population scale, in the second section, I studied individual features that may affect the potential for adaptive changes in migratory behaviour in a model species, the blackcap *Sylvia atricapilla*. This second section is based on field data collected between 2010 and 2012 on a partially migratory population of Blackcaps from Eastern Spain.

The results of this thesis can be summarized in 13 main findings [chapters in bracket]: (1) At least 41 out of the 80 studied species of European trans-Saharan migratory birds have established wintering populations north of the Sahara [I to IV]. (2) In most species, these populations have significantly increased in the last decades [II, III]. (3) Coastal wetlands are hot-spots where most of these new wintering individuals occur [I, II]. (4) Species that have larger wintering ranges in Africa and arrive early in spring to Europe are more likely to establish wintering populations

north of the Sahara [II]. (5) Non-passerines showed a stronger adaptive response than passerine species [I to III]. (6) Temperature trends in Europe in the last decades are not related to the incidence of wintering of trans-Saharan migrants north of the Sahara [III]. (7) Once trans-Saharan migrants have established wintering populations north of the Sahara, the northern limit of the new wintering range continues to gradually shift northwards [IV]. (8) There is undetected phenotypic and genetic variation in the pattern of juvenile moult of Blackcaps [V]. (9) Resident Blackcaps, which probably descended from a migratory lineage during the last glaciation, still have migratory appearance in their flight-related morphology [VI]. (10) Residents and migrants from a partially migratory population do not differ in migration-related plumage morphology [VI]. (11) When sharing a wintering territory, resident Blackcaps are dominant over migrants, despite their smaller body size [VII]. (12) Resident and migratory Blackcaps have differently composed winter home ranges but the same habitat preferences [VII]. (13) The composition of the wintering population suggests the occurrence of sex-biased and environmental-dependent partial migration [VII].

Overall, the results presented in this thesis are consistent with the predictions on adaptive shortening of migratory distances that European trans-Saharan birds need to realize in order to advance spring arrival in response to phenological changes observed under recent climate change. Our data support that this shortening of migration distances at a flyway scale had occurred and is still on-going, at least in species that have more flexible migratory programmes. Population-scaled studies from this thesis contributes to elucidating the specific mechanisms that fuel adaptive potential of migratory behaviour, and will be a solid basis on which to formulate future predictions about the consequences that these changes will have on migratory birds in general.



General Section

Photo © Ugo Mellone www.wildphoto.it
A wintering heron at the Kalamas delta, Greece.

1. Introduction

1.1 From long-distance to partial migration: all the birds on the move!

Seasonal movements of varied magnitude, generally performed between regions where conditions alternatively are favourable and unfavourable, have evolved and become established in many animal species from any branch of the phylogenetic tree, taking the name of *migration* (Dingle and Drake 2007, Newton 2008). However, it is in the class *Aves* that migration is most conspicuous, in terms of covered distances, complexity of routes and magnitude of the phenomena: 2.1 billion birds are estimated to migrate every year only between Europe and Africa (Hahn et al. 2009). Long-distance migration is likely to have emerged early in the evolution of birds and there is evidence for its presence in some groups, like the *Scolopacidae* (waders), before the Pleistocene (Matthiensen 1990, Louchart 2008). In evolutionary terms, migration is probably as old as birds themselves (Berthold 2001).

Benefits of migration mainly relate to the possibility to profit from the continuous availability of resources, without interruption throughout the annual cycle, by tracking the peak of maximum productivity of ecosystems at a planetary scale (Alerstam 2003). This type of migrants literally lives in an "endless summer" (def. by Shaffer et al. 2006). For instance, the Arctic tern *Sterna paradisea* breeds north of the Arctic Circle and winters south of the Antarctic Circle. Thus, this bird tracks foraging opportunities throughout the globe and lives in constant light almost during its entire life, except during migration, when it must cross intermediate latitudes (Egevang et al. 2009). However, not only the need of tracking food but a complex net of selective pressures have determined the evolution of migration (Dingle and Drake 2007). Otherwise, it is hard to explain why birds that live most of their life in tropical latitudes migrate for reproduction thousands of kilometres. In these species, the avoidance of intra- and inter-specific competition is a strong reason to leave the overcrowded tropics and migrate to the much less crowded areas in the north. But, not only tropical birds may face competition. Birds from middle latitudes may need to leave their breeding sites during winter because their breeding quarter is invaded by migrating and wintering conspecifics from northern latitudes (Bell 2000, Pérez-Tris and Tellería 2002), making these area unsuitable for wintering because of huge competition even if food availability and winter temperature alone may would not be limiting factors in absence of concurrent wintering birds.

An extraordinary example of a life-history shaped by migration is the case of the Eleonora's falcon (*Falco eleonorae*). This falcon not only performs extraordinary migratory movements but its lifestyle is fully dependent on the migration of other birds, because it exploits the feeding niche offered by the concentrations of migratory songbirds on the small islands of the Mediterranean Sea during fall migration (Cramp and Simmons 1998). To do so, it syn-

chronizes its reproduction with the peak of fall migration (late August – September), being among the latest European bird species to reproduce (Cramp and Simmons 1998). However, Mediterranean islands do not offer many resources during winter, thus Eleonora's Falcon need to migrate. During its migration, it crosses Africa tracking the availability of insects during autumn, and finally overwinters in Madagascar, where productivity is at its maximum during the boreal (Mellone et al. 2012, 2013). The extreme cases of the Eleonora's Falcon and the Arctic Tern should not obscure the fact that migration does not necessary imply crossing the globe. Actually, most birds profit from their large mobility just to move some kilometres, to descend from a mountain, or to move from a rural habitat, where they reproduce, into warmer adjacent urban habitats (Berthold 2001). On a wider geographic scale, many species show variation in migratoriness depending on breeding latitude, as found in the *Paridae*, which are mainly sedentary in southern but largely migratory in northern Europe. In the blackcap (*Sylvia atricapilla*), among-population variation in migratoriness ranges from total residency to long-distance migration (Shirihai et al. 2011). Recent studies demonstrated that even tropical species that were thought to be sedentary show certain degree of migratoriness, so that at least a few individuals within the population migrate, revealing previously unknown patterns of partial-migration (Jahn et al. 2010b). Ultimately, this means that all birds are on the move and insights on the factors shaping and affecting migratory patterns may be relevant not only for a reduced group of so-called migratory species but for birds in general.

1.2 Winged migration in a changing world

Contemporary climate change is evident (IPCC 2007), and it directly or indirectly affects a wide range of biological features of living organisms all over the earth (Parmesan and Yohe 2003, Parmesan 2006, Letcher 2009). Migratory species are expected to be among the most affected organisms because they have complex life cycles in which successive phases are spent in different geographical areas (Robinson et al. 2009). To stay with the previous example of Eleonora's Falcon: it is easy to understand that the set of selective pressures that shaped such a life-history are finely tuned on the spatial distribution of climatic niches over the globe. This implies that populations of this species are extremely sensitive to any spatial shift of the climate zones in which they live. Indeed, climate change is shifting the distribution of the climatic zones towards the poles (IPCC 2007), exposing Eleonora's Falcon, as well as all the other migrants, to fundamentally different selective regimes. Populations of these species have no other choice than to move away or adapt to the new conditions, or perish. In this light, new selective regimes imposed by climate change represent new challenges, when not a serious threat, for the conservation of migratory birds (Berthold et al. 1998; Both et al. 2006; Møller et al. 2008; Saino et al. 2011).

Migratory patterns are to some extent flexible (Sutherland 1998, Newton 2008). This is valid both at the individ-

ual and at the population level (Pulido 2007a,b). A single individual is able to adjust its migration to the external conditions it encounters, such as wind (Erni et al. 2005), but also some features characterizing the migration of an entire population or species may change over evolutionary times in response to changes in the selection regime, as could be the northward shifting of the wintering ground (Lehikoinen et al. 2013). A long list of changes in migratory patterns have been compiled nowadays and involve alterations of the migratory route, shortening or lengthening of the migration distances achieved by moving or expanding winter or breeding ranges and, especially, changes in timing of migration (reviewed in chapter21 in Newton 2008). In particular, this last aspect has received most of interest because it is thought to be this particular migratory feature that is most affected by climate change (Knudsen et al. 2011). Both timing of migration and timing of arrival at the breeding grounds have advanced in the last decades (Lehikoinen et al. 2004, Jonzén et al. 2006, Rubolini et al. 2007, Végvári et al. 2010). These changes are likely to be a response to increasing spring temperatures across Europe (Both and te Marvelde 2007, Knudsen et al. 2011). However, climate change also affects conditions in the wintering quarters and the areas of passage. The role of these changes in determining the new selective regimes is less understood than the impact of spring warming in the areas of reproduction (Gordo 2007). The advancement of spring arrival has been sometimes associated with a delay of autumn departures (Lehikoinen et al. 2004, Lehikoinen and Jaatinen 2012), possibly meaning that at least some species of short-distance migrants are experiencing a lengthening of the reproductive season (Jaffré et al. 2013). Evidences on long-term trends in phenology of autumn migration are anyhow less clear than the general advancement reported for spring arrivals (e.g Adamik and Pietruszková 2008). Long and short distance migrants in particular repeatedly appeared to respectively advance and delayed (or not change) departure dates from breeding grounds (Jenni and Kéry 2003, Mezquida et al. 2007). As a result, data from different sites may report opposite results, per example estimating that duration of reproductive season has not changed (Thorup et al. 2007). Another large body of evidence shows that short and middle- distance migrants are moving their wintering quarters northwards, thus shortening migration distance (Visser et al. 2006, la Sorte and Thompson 2007, Lehikoinen et al. 2013). Short-distance migrants are also the group of birds that most strongly have advanced phenology of migration (Rubolini et al. 2007, Végvári et al. 2010) and begin of reproductive season (Rubolini et al. 2010). Taken these evidences together, we can make the overall prediction that climate change promotes an advancement of spring arrival which could be achieved by a northward shift of the wintering quarters.

Thus, once again, it is evident that migration patterns are not fixed and that climate change can shape migration timing and routes and the location of wintering areas. In evolutionary times,

climate change has probably been one of the most important determinants of migration patterns. Indeed, repeated oscillations in climate regimes during the Pleistocene (about 2.6 Myr – 10,000 years) are claimed to have caused continuous adaptive changes of migratory habits in all the lineages of birds living in this period (Bruderer and Salewski 2008). Thereafter, re-colonization from southern refugia during the warming period that followed the last glaciation (last 10,000 years) led to the contemporary latitudinal distribution of populations with growing degree of migratoriness in northern hemisphere (Newton 2008 and specific cases in Peréz-Tris et al. 2004, Milá et al. 2006). Thus, the question is no longer if migration can change but whether migratory species will be able to adapt to the contemporary climate change or go extinct. The capacity to develop adequate responses to cope with new selective pressures is often expressed in terms of *adaptive potential*.

1.3 A general model of the adaptive potential of migratory behaviour

Adaptive potential is defined as the capacity of populations to adapt to environmental changes, measured as the extent to which populations are able to make adaptive phenotypic changes to cope with new selective pressures. This capacity is considered to be also fuelled by phenotypic diversity and plasticity but mainly by genetic diversity (Willi et al. 2006). However, phenotypic plasticity may be sufficient to achieve the phenotypic changes needed to cope with a specific selective pressure (Merilä 2012). Thus, both genetic variability and phenotypic plasticity fuel the adaptive potential of populations. These two features have phenotypic effects usually impossible to distinguish between them with the types of data generally collected (Merilä 2012). As a consequence, to date, conclusive examples of (genetic) evolutionary changes in response to climate change are extremely scarce (e.g. Balanyá et al. 2006, Pulido and Berthold 2010, Karell et al. 2011). Adaptive potential is sometimes used as synonym of *evolvability* (Houle 1992, Brown 2013), a concept that should strictly indicate the capacity for generating heritable phenotypic variation (Kirschner and Gerhart 1998), irrespective of the possible adaptive value of this variation. Conceptual differences between the terms evolvability and adaptive potential reflect the problems in distinguishing the occurrence of evolutionary changes or plastic response underlying an observed phenotypic change. This problem has major evolutionary consequences, given that the amount of plasticity of a genotype is limited while (adaptive) evolutionary changes can move further away. Ultimately, this may be crucial for the conservation of a species, because populations showing an evolutionary response are likely to persist over evolutionary times, while populations that rely only on their adaptive plasticity may run out of adaptive potential and go extinct, sooner or later.

Bird migration offers a great subject on which to study this problem. Evidences from all over the world describing phenotypic changes in migratory behaviour of birds are nowadays abundant (see examples above). Overall, this bulk of

evidence suggests that migration features, like migration routes, timing, and the spatial location of wintering and breeding grounds, may readily change in response to external selective pressures, as the ones imposed by climate change. However, even if exposed to the same selective pressures, some species may show adaptive changes of migratory features, while others may not, as demonstrated in a few studies comparing the reaction of vast set of populations from the same geographical area (e.g. Visser et al. 2009, Rubolini et al. 2007, Végvári et al. 2010, Gordo & Doi 2012a, b). This is the case, for instance, in short and long-distance migrants that breed in the same area and that are both exposed to selection favouring the advancement of spring arrival but only the first group effectively advance its arrival (e.g. Végvári et al. 2010). Comparing evidence of realized and non-realized changes permits the formulation of a simple model describing the expected capacity of bird populations to adaptively change their migratory features in response to external selective pressures (Figure 1). Such a model may help formulating expectations and testing specific hypothesis regarding the adaptive capacity of migratory behaviour of a given population or species. In the model, the term "migratoriness" is used to indicate at the same time the proportion of migrants in a population and the mean migration distance of that population. The two parameters are related and can be expressed in a single continuous axis (Pulido et al. 1996, Pulido 2011). Despite its continuous character, migratoriness can be classified in three main categories to facilitate interpretation (residents, partial-migrants and long-distance migrants). Starting from the resident extreme of the curve, below the migration threshold, genes controlling for migration are not expressed (resident populations) even if present in the gene pool of the population, resulting in phenotypic uniformity of the individuals (Pulido et al. 1996). In this situation, natural selection cannot "remove" migration genes, and genetic variability on migratoriness is maintained (Pulido 2011): in other words, "migration genes" are likely to be present also in fully resident populations, ultimately pushing well above zero the amount of their adaptive potential on migration-related features (Figure 1). While in a resident population phenotypic homogeneity
in migratoriness is achieved because it lays under the threshold of its expression (Pulido et al. 1996), at the other extreme of the curve (i.e. long-distance migrants) phenotypic homogeneity is determined because phenotypic variation on migratory patterns is canalized (Pulido and Widmer 2005), possibly as a consequence of strong stabilizing selection. Even if genetic variance in migratory traits in these populations may not be reduced (Pulido 2007b), the potential of phenotypic adjustment by phenotypic plasticity is reduced. Hence, the adaptive capacity is reduced. Moreover, the expression of migration is tuned on external cues that are not altered by climate change (as photoperiod), so these species are possibly unable to respond to the changes in climatic parameters relevant for their fitness (Coppack and Pulido 2004). Inability of

long-distance migrants passerines to undertake adaptive changes of migratory patterns had been repeatedly suggested (Sutherland 1998, Pulido and Widmer 2005) and confirmed, at least, in the arrival dates of one population of Pied flycatcher (*Ficedula hypoleuca*, Both and Visser 2001). On the other hand, partially migratory populations are supposed to be the ones in which genetic variability on migratory traits is maximal, and represents a "behavioural turntable" for micro-evolutionary processes on migratory behaviour (definition by Berthold 1999). These considerations shape the blue curve of Figure 1 that shows higher adaptive potential for resident compared to long-distance migrant populations, and partially-migratory ones with the highest value among the three groups.

The above arguments are based on the assumption that migratory behaviour is mainly genetically determined. However, although this assumption fits well the findings about night-migrating passerines that show migratory restlessness (*Zugunruhe*), it hardly holds when applied to large long-lived species, in which control of migration is mainly socially and environmentally mediated (e.g. Mueller et al. 2013). In these species, even if a component of inherited migratory program can be found, this needs to be tuned by social information, as obtained by following experienced birds during the first autumnal migration (Chernestov et al. 2004). Thus, different predictions need to be made for birds with a predominant genetic control of migration and for birds in which migration is primarily environmentally controlled. Throughout this thesis, the coarse but clear distinction in "*passerines"* and "*non-passerines"* will be used to account for this difference. Even if this classification is phylogenetically inaccurate ["*passerines"* refers to one specific order (*Passeriformes)*, while non-passerines include all other orders of the class *Aves*], it is effective because the two groups roughly represent the two different systems of migration control. Therefore, for predicting the adaptive potential of migratory behaviour among non-passerines species, a second curve needs to be drawn (green curve in Figure 1). As a consequence of the important role of plasticity and environmental stimuli in the determination of migratory patterns among non-passerines, the adaptive potential is expected to be higher than for passerines throughout the range of migratoriness. Moreover, for this group of species, differences in genetic variability related to migratoriness would only have a minor effect in determining the amount of adaptive potential. As a consequence, populations of non-passerines that differ in migratoriness are expected to only slightly differ regarding adaptive potential of migration. This results in a more flattened curve than for passerines. Throughout this thesis, three out of the six groups of birds identified in Figure 1 will be treated: long-distance passerine and non-passerine migrants (Section I), and partially migratory passerines (Section II).

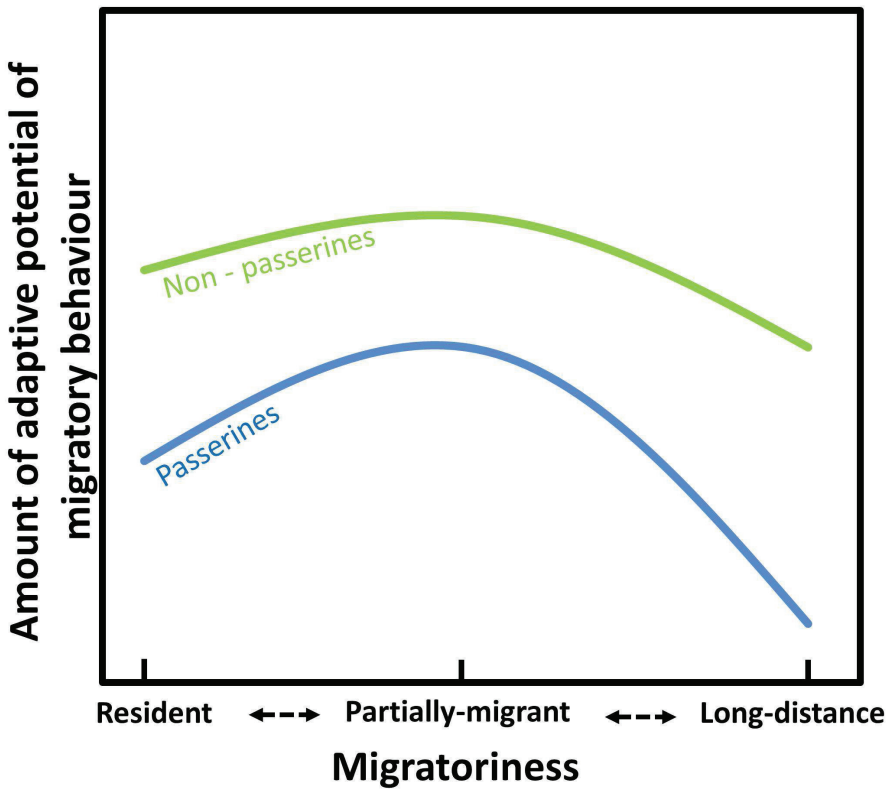


Figure 1

Predicted adaptive potential of migratory behaviour of bird populations differing in migratoriness. Depending on the selective regimes, wild populations may adaptively increase or reduce migration distance and the proportion of migratory individuals in the population, as arrows indicate. Partially-migratory populations maintain a high degree of genetic and phenotypic variability in both traits, thus having the highest adaptive potential. At the extremes of the distribution, canalization is expected to reduce phenotypic variance and plasticity, resulting in a reduced adaptive potential for long-distance and resident populations. However, among long-distance migrants, canalization is considered to be stronger, so that the amount of adaptive potential in this group is further depleted if compared to resident populations. Passerines (in blue) and non-passerines (in green) differ in the degree of genetic determination of migratory behaviour, having as a consequence that adaptive potential in the latter is constantly higher and differences between populations at different degree of migratoriness less accentuated in this group (more flattened curve for non-passerines). Overall, adaptive changes of migratory behaviour are expected to be maximum for partially migratory populations of non-passerines and near to zero in long-distance passerines ones.

1.4 Specific model of the adaptive shortening of migration distance in European migratory birds facing climate change

The shortening of migration distance has been suggested as a possible adaptive response of migratory birds to climate change (Berthold 1998, Berthold 2001, Coppack and Both 2002, Pulido & Berthold 2004, Pulido 2007b), given that this would cause an advancement of arrival at the breeding quarters, which is favoured by climate change. This prediction can easily be translated into a specific model predicting the shortening of migration distance in birds that migrate along the Western European flyway (Figure 2).

Given that strong selective pressures imposed by climate change are expected in Europe during the reproductive season of birds (e.g. Ockendon et al. 2013), both long and short-distance migrant should be equally exposed to these pressures. However, trans-Saharan migrants face a further problem, given that the unsuitability of the Sahara for overwintering hampers the eventual gradual northward shift of the wintering grounds. Thus, distinct predictions can be made for these two groups of migrants (the two lines of Figure 2).

According to the predictions of the threshold model of migration (Pulido et al. 1996), shortening of migration distances by moving the wintering area northwards should occur gradually, in parallel to the progressive reduction of migratory fraction of the population, and can continue until complete residency or partial migration is achieved and winter and reproductive ranges overlap (steps SD1 To SD3 in Figure 2). Evidence from both Europe and North America show that this is being happening in short-distance migrants, which find suitable wintering areas along all their migratory route (Valiela and Bowen 2003, La Sorte and Thompson 2007, Maclean et al 2008, Visser et al. 2009, Lehikoinen et al 2013). For European long-distance migrants such a progressive shift is hampered by the Saharan desert, and this means that after a progressive northward shifting of the wintering area within Africa (as described for *Hirundo rustica* by Ambrosini et al. 2011), they need to undertake a sudden shortcut of the migration and start to winter in the Mediterranean Basin (step LD3 in Figure 2). Even if exists sporadic reports of trans-Saharan migrants the wintering in Mediterranean basin (Berthold 2001, Sutherland 1998), it is unknown if this is a general trend and which species are able to do it, as indicate the questions marks in box LD3 of Figure 2. To go on, for populations of European long-distance migrants that finally establish wintering population in Western Mediterranean, if selection towards residency persists, migration distances are predicted to continue their shortening until the condition of partial-migrants or residents is achieved (i.e. breeding and wintering quarters overlap, steps SD1 to SD3 in Figure 2).

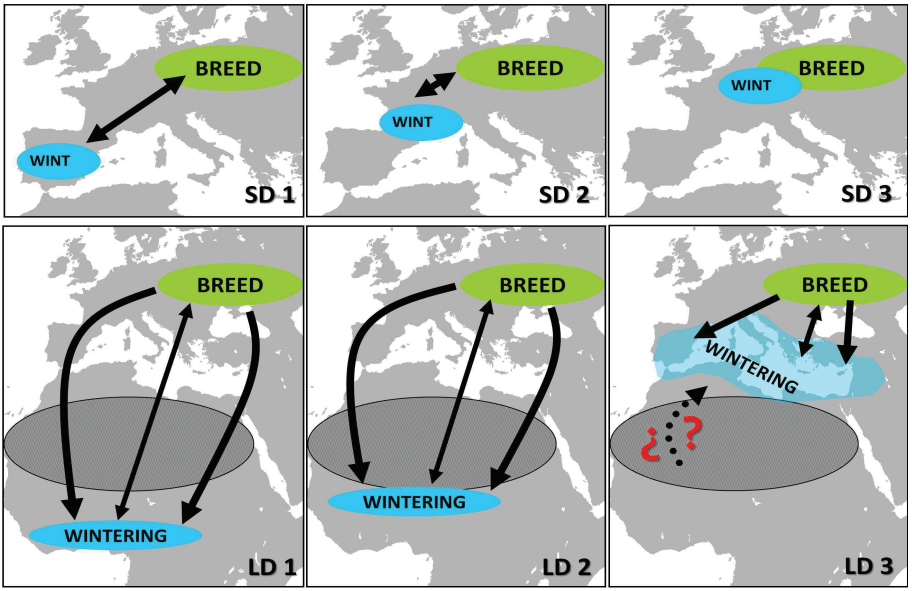


Figure 2

Model of the shortening of migration distance in response to climate change for European migratory birds. In the figures SD1-SD3, a model for middle and short-distance migrants (SD) is shown. In the first step (SD1), the hypothetic species breeds in north-east Europe and winters in Iberia. As a response of climate change the progressive shortening of its migration distance is achieved by northward shifting of the wintering range (SD2). Eventually, wintering and breeding grounds partially or completely overlap, meaning that at least some populations of the species became resident or partial-migrants. Today, there are many studies suggesting that step 1 to 2 had occurred (see refs in the text and in Chapters I to IV). The figures LD1-LD3 show how a progressive shortening of migration distance may be achieved by long-distance migrants (LD). In step 1, the normal situation is given: European breeding quarters are abandoned to cross the Sahara (shaded area) and winter in the Sahel, as most of the trans-Saharan European birds. In step 2, the wintering area has moved northward, reaching the southern edge of Sahara. The next step cannot be gradual anymore, given that Sahara is not a suitable area for wintering, and an abrupt shortening of migration distance is needed to start wintering north of the Sahara.

2. Objectives

The main aim of this thesis is to give new insights on the capacity of migratory birds to adapt to global change. To fulfil this aim, I followed a top-down approach both at a spatial and at a temporal scale, i.e. from regional to local scale and from long- to short-term periods. In the first section, I explored patterns and potential causes of the shortening of migration distance in European trans-Saharan migrants. This large-scale long-term study involved many of the Palearctic migratory species of birds. In particular, I addressed the following questions:

(1) Are long-distance European migrants shortening their migration distance by establishing wintering population north of the Sahara? (Chapters I and II)

(2) Is it possible to identify hot-spots that need higher degree of protection for the increasing phenomenon of wintering of trans-Saharan birds in Europe? (Chapter I)

(3) Have the populations of trans-Saharan species wintering north of the Sahara increased or remained stable in the last decades? (Chapter II and III)

(4) Which ecological features determine the probability of a species to show an adaptive shortening of migration distance? (Chapter II)

(5) Do passerine and non-passerine long-distance migrants differ in their adaptive capacity when facing selection favouring a shortening of migration distance? (Chapter II)

(6) Is the observed shortening of migration distance related to climatic warming in the last decades? (Chapter III)

(7) Are populations that have established wintering quarters in Europe moving their wintering ranges northwards? (Chapter IV)

Given that adaptive processes happen at the population scale, the second section is dedicated to explore individual features that may be affecting selection of migratory behaviour at a local scale. For this purpose, I studied a partially migratory population of Blackcaps from Eastern Spain. Specific questions addressed in this section were:

(1) Is there phenotypic and genetic variation in a life-history trait traditionally considered invariable? (Chapter V)

(2) How strong are selective pressures related to migratory behaviour acting at the morphological level? (Chapter VI)

(3) What are the behavioural consequences of different migratory strategies in a wintering quarter shared by local residents and northern migrants? (Chapter VII)

(4) Do the complex dynamics of coexistence established in wintering areas generate a pattern for which individual differences in key features (e.g. age, sex, body size) are reflected in behavioural differences, ultimately promoting the maintenance of a large variability in migratory behaviour within a single species? (Chapter VII)

3. General Methods

Methodologies of the two sections are completely different and for this reason are treated separately. Statistical analyses are commented in the specific part of each chapter and not mentioned here.

3.1 Methods of Section 1

3.1.1 A vast data recompilation: selection of species and space-time window

In order to explore middle to long-term evolution of the wintering of trans-Saharan migrants north of the Sahara, I had to build a database that included all available information around the subject.

The first step was to select the area on which to focus the search. Given the focal relevance of the Mediterranean basin for wintering of Afro-Palearctic migrants (Handrinos and Akriotis 1997, Cramp and Simmons 1998, Berthold 2001, Spina and Volponi 2008, SEO/Birdlife 2012), the Iberian Peninsula is a good candidate region where we would expect to find long-distance migrants that shortened their migration distances. I thus decide to gather information regarding the geographical range of Iberian Peninsula, successively including also Morocco until the 27º N of latitude, considered as the northern border of the Sahara desert.

Bibliographic search aimed to gather all published information about trans-Saharan migrants wintering in this range. For this search I could use the library of the *Sociedad Española de Ornitología* (SEO), which collects all the ornithological publications from the Iberian Peninsula and Morocco since 1959. This search was complemented by an extensive web search and, when necessary, by publications directly made available by the authors. Most of the consulted publications contained valuable information but many others did not. Supplementary material of Papers II and III report the full list of publications from which I gathered information.

The second step was to select those species relevant and suitable for the intended analyses. The concept of trans-Saharan embraces species differing in their wintering range, migration phenology and proportion of the world population that crosses the Sahara during migration. I finally selected 80 species using as a requisite the fact to be considered fully trans-Saharan at least in the Cramp's encyclopaedia (Cramp and Simmons 1998). I also paid attention in build the list of species trying to cover the whole phylogenetic range, so that some species of waders unclear breeding status in Europe but that certainly migrate across it and considered fully trans-Saharan migrants, were included too (i.e. *Calidris ferruginea* and *Tringa stagnatilis*).

The last step was to define the study period. Oldest records in the database date back to 1867, but only 22 data (constituting the 0.002% of the whole database) were collected before 1950 and less than 0.5% were anterior to 1968, clearly showing a poor coverage for this time span. I have thus considered as representative data, describing

the on-going situation, those observations which were made after 1968. Due to the delay in the publication, in 2008-2010 -when the bibliographic search was carried out-, much information about the last years was not available, generating a decline in the amount of available data. I thus limited the time window to 2006 to avoid this problem. Figure 3 depicts the geographic range and time span for which data were collected. Further details on data selection and use are given in the respective chapters. The final list of the 80 species selected is given in Table 1 of Chapter I. Depending on the type of data required, different subsets of species were considered in each Chapter or analyses.

3.1.2 Establishment of species-specific wintering windows

Due to the inter-specific differences in migration phenology, was necessary to define species-specific periods in which consider the observations as true wintering episodes. We established this window according to the migration dates across the Strait of Gibraltar (based on Bernis 1980, Tellería 1981 and Finlaynson 1992). Table 1 of Chapter I show the species-specific time windows for all the 80 species considered in this thesis. Even if falling into the wintering window, we excluded all the records in which the observer explicitly suggested a possible very late or very early migrant, as well as records based on animals found dead.

3.1.3 Quantitative and qualitative analyses of trends in wintering events

Trend in the number of wintering episodes of trans-Saharan species in Iberia and Morocco was explored in a quantitative way, by testing regressions between the overall number of wintering events and the year (Chapter II), or separately passerines and non-passerines (Chapter II), or individually for each species (Chapter III). In all the cases, autoregressive terms were introduced in the regression model to control for the effect of temporal autocorrelation (see Methods of Chapters II and III).

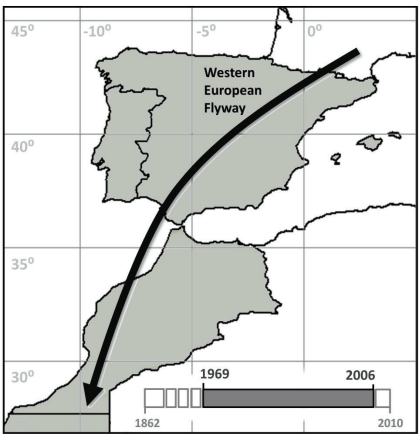


Figure 3
Location of the study area along the end of the Western European flyway. Shaded area was considered for the collection of data on the wintering of trans-Saharan species. Southern limit of 27ºN coincides with the border of the figure. Data were collected between 1968 and 2010, but the analyses were based on data from the period 1969-2006.

Moreover, a qualitative assessment of the trend was also performed, by dividing the considered time period in equal sub-periods and assigning a score for the regularity and the "intensity" of observations for a particular species within each period. Thus, for each species and period, a score ranging from 0 (species not established at all in winter) to 4 (fully established wintering species) was assigned. This approach is more conservative than the pure quantitative one, because it permits to define for each period if the presence of a species in winter was accidental or represents the occurrence of established populations.

3.1.4 Ecological and phenological traits

In order to analyse which ecological and phenological specific traits would promote different ability in establish wintering populations at north of the Sahara (Chapter II), I compiled a database that summarized these features for the set of species object of the analysis. I based this compilation on information provided in Cramp and Simmons (1998), from which I extracted data on the spatial distribution of breeding and wintering range as well as on the phenology of migrations and reproduction. Data was collected considering a year composed by 12 months of 4 weeks each and assigning the progressive number 1 to 48 to the weeks, following the approach used in the phenological diagrams of Cramp and Simmons (1998). From this book, I gathered data on specific mean body size too. Overall, I compiled a list of 21 variables that were reduced to few variables by the means of a principal components analysis (PCA). The effect of the resulting principal components on the probability of a species to establish wintering populations at north of the Sahara was tested in a model that allow to control for phylogenetic relationships among species. Selection of the best model was performed following AIC criteria (Akaike 1973). Further details on this analysis are available in Chapter II.

3.1.5 Direct link with climate warming

Chapter III was dedicated to explore the potential link between temperature trends in Europe and north-Saharan wintering quarters and the increasing in the number of records of trans-Saharan birds wintering in the western Mediterranean. I considered temperature trends between 1969 and 2006 experienced in: reproduction, fall migration and wintering. Specifically, four hypotheses were tested: 1. Increased temperatures in the new north-Saharan wintering quarter enhance probability of winter occurrence; 1(b). Winter temperatures predict wintering probability with a delay of 1 year because winter survival determines whether individuals will overwinter again or not; 2. Temperatures experienced in south-western Europe during fall migration determine the decision to stop migration and overwinter there or to keep on migration; 3. Increases in spring temperature in the breeding areas induce individuals to winter closer to the breeding sites in the following winter. In this analysis 77 species were considered and, for each one, temperature trends were calcu-

lated for species-specific geographical areas and phenological time windows. Then, a model was run for each species to test if any of the four temperature trends significantly explained the oscillation in the number of wintering individuals north of the Sahara. Models were repeated twice using a wider and a narrower time window considered for each life phase.

3.2 Methods of Section 2

3.2.1 The Blackcap as a model species

The Blackcap (*Sylvia atricapilla*) is a common subject for avian studies. The huge amount of knowledge about this species makes it an ideal model to study the mechanisms underlying the adaptive potential of migratory birds at a population scale. The Blackcap is one of the most common breeding species of Western Palearctic and presents wild populations in which migratory behaviour spans from completely sedentary (e.g. Gibraltar area population) to long-distance migratory (e.g., in northern Europe; Shirihai et al. 2001). This fact offers the possibility to study causes and consequences of migratory behaviour controlling for the species effect, by comparing different populations from different breeding areas. Moreover, the past evolution of the migratory behaviour across Europe of the species is known, being associated to a re-colonization from glacial refugia in southern Spain during the warming period of the last millennia (Pérez-Tris et al. 2004). The genetic basis of migratory behaviour in the species had been studied in populations from the whole breeding range through *"common-garden"* experiments, in which behavioural differences in birds raised in the same environmental conditions need to be genetically determined (Berthold and Querner 1981, Berthold et al. 1990, Pulido et al. 2001, Berthold and Helbig 2008). The same common-garden approach was used to study a single partially migratory population from Southern France but in this case quantitative genetic arguments did not fully account for the observed patterns, suggesting that environment must play some role in make an individual resident or sedentary in these populations (Berthold 1986). Results from experiments with captive Blackcaps are at the basis of the modern conceptual models of the control of migration, (the *threshold model*, Pulido et al. 1996) that recently have been improved to include the role of the environment in determining the migratory status of a population (Pulido 2011). Moreover, difference in migratory behaviour in Blackcaps have been associated to morphological differences in flight morphology (Fiedler 2005), so birds belonging to different breeding areas are easily distinguishable even if they are mixed in sympatric wintering grounds (Pérez-Tris et al. 1999, de la Hera et al. 2007), making it a suitable subject to study the effect of intraspecific competition at wintering quarters. Furthermore, a lot is known about behaviour of Blackcaps, and Iberian populations are particularly well studied (e.g. Jordano and Herrera 1981, de los Santos 1986, Rey 1995 and 2011, Tellería and Carbonell 1999, Pérez-Trís et al. 1999 and 2004, Pérez-Tris and Tellería 2002, de la Hera 2007 and 2012, Tellería et al. 2007, 2008 and 2013).

3.2.2 Study area

Study area was located along the riverbank of the Serpis River, in the municipality of Cocentaina (38º 44' N - 0º 44' W. Province of Alicante, Region of Valencia, Eastern Spain, Figure 4). Landscape is a typical hilly Mediterranean environment (400-500 m a.s.l.), widely exploited for olive groves and characterised by scarce broadleaf vegetation, which is mainly concentrated on the bottom of the valley. This area was selected because we considered it to have high probability of finding partial migration in local populations. This expectation was based on the fact that (i.) previous studies conducted in nearby areas shown that abundant contingents of Blackcaps were wintering there (Leal et al. 2004); (ii.) local ringers had observed that Blackcaps were scarce but present as breeders along the riverbanks of the area (Domínguez M, Cantó

Figure 4

Location of the study area (left) and a panoramic view of the Valley of the River Serpis (up) in winter 2012. The leafless poplars crossing at the middle of the image mark the river position. Photo and image by Giacomo Assandri.

P, Limiñana R and Pérez-García JM pers. comm.); (iii.) latitudinal location of the area is in between partially migratory populations (with a high proportion of migrants) in Southern France (Berthold 1986) and completely sedentary populations in southernmost Spain (Pérez-Tris et al. 2004). For all these reasons, we expected that migratory behaviour of this population would be partially-migrant.

3.2.3 Field protocols

Field work was developed on 5 field seasons between 2010 and 2012 (breeding seasons 2010, 2011 and 2012, winter seasons 2010-2011 and 2011-2012). I considered as breeding season the period between the 20th of March and the 15th of August, and as wintering season the period between the 20th of November and the 25th of February. Field work was structured in four main activities: i) individual capture-recapture, ii) behavioural observations, iii) monitoring of breeding activity and reproductive parameters, and iv) individual telemetry by radio-tracking. Individual capture-recapture was carried out by mist-netting during the whole day at various points within the study area, particularly at feeding sites or within individual territories, which were previously identified by singing males. Within and between seasons, some net positions were repeatedly used, in order to exhaustively sample the locality and maximize recapture probabilities. When needed, tape-luring was used to improve capture rate. Blackcaps were aged and sexed according to their plumage characteristics (Jenny and Winkler 1994). Each bird was marked with a numbered aluminium ring and three colour rings. Each combination of rings was unique, which allowed the remote identification of each individual by observation. Before release, morphological measurements (length of tarsus, wing, 8th primary and beak as well as indexes of muscular development and fat content) of each bird were taken following standard ringing methodologies (Svensson 1992). Birds were also weighted. All birds were released at the site of capture immediately after manipulation.

Behavioural observations were performed at feeding places (fruit-bearing pomegranate, *Punica granatum,* shrubs and, kaki, *Diospyros kaki,* trees) mainly during winter, when flocking behaviour and lack of foliage facilitated observations. In order to maximize re-sighting probabilities, identification of Blackcaps was also attempted at any given occasion during the reproductive seasons (e.g. when heard a singing male or a Blackcap call).

During the reproductive seasons of 2011 and 2012, nest-searching was performed in each territory (identified by a singing male). Once a nest was found, a hidden camera and/or mist-net was used to identify the parents (see Morganti 2013 and http://www.youtube.com/watch?v=EnllFEgz940; http://www.youtube.com/watch?v=LKy26W8fEzI; http://www.youtube.com/watch?v=B-kxUm9z10s). When possible, chicks were ringed and nests where checked every second day until chicks fledged. Spring data were used in this thesis only to delineate capture/recapture histo-

ries of individual Blackcaps for the classification in Wintering/Migrant/ Resident used in of chapter VI (see below). The discriminant function analysis described in Chapter VI was based on the classification of Blackcaps in local yearround residents (named as "R"), northern European birds wintering in the area ("W") and migrants of the local breeding population ("M"). Figure 7 in Results shows the conditions that individual capture-recapture histories had to fulfil to be classified in one of the three groups.

3.2.4 Radio-tracking and home range calculation

In order to study home-range size and structure both during reproduction and wintering, birds were equipped with PicoPip radio trasmitters of Biotrack (www.biotrack.co.uk), attached with a rubber harness that falls off after a few weeks (Rappole and Tipton 1990). Weight of the whole pack (harness + emitter) was less than 0.5 g, thus lower than 5% of the mean Blackcaps weight (overall mean weight = 17.54 ± 0.84 g; N=1125). Radio tracking was performed during the reproductive seasons 2011 and 2012 and during the wintering seasons 2010-2011 and 2011-2012. Transmitters were installed at the beginning of each season. Radio tags fallen off because of premature rupture of the harness were reused by attaching it on a different bird. Tracking was conducted by locating the birds through triangulation and progressive approaching until the position was determined with no doubt, but taking care to not chase away the bird. Locations of birds were determined once or twice per day, paying attention in obtaining locations during each hour of the daylight, in order to describe the movement of the whole day. Locations were taken until the end of the life of the emitters or the end of the studied season. At the end of the tracking period, all the locations obtained for each individual were merged into a unique home-range, which was considered to represent the home range used throughout the season. Home ranges were calculated as fixed kernels at 95% using the "HRT tools" extension (Rodgers et al 2007) for ArcGis 9.3 (ESRI, Redlands, CA, USA). Smoothing parameter of the kernel (href) was individually-adjusted by selecting the smallest value of href, rounded to the nearest 0.05, for which the external boundary of the kernel remains continuous, following the progressive method described in the HRT tools manual (Rodgers et al. 2007).

3.2.5 Common-garden experiments

In order to determine how much genetic variation there is in life-history or behavioural traits we performed a common-garden experiment, in which we maintained in captivity 31 first-year Blackcaps collected in Cocentaina as chicks. Birds were maintained in identical conditions, being exposed to natural photoperiod and having unlimited availability of food (fruit, mealworms and birdseed). Moult status of the birds was established by quantifying the number of growing feathers both in wings and body, following the classification scale in Jenni and Winkler (1994). Differences in the moult pattern between these birds are likely to be due to genetic variation, given that envi-

ronmental variation is controlled. With this method, in Chapter V, I studied the occurrence of previously undetected genetically-determined variation in juvenile moult pattern, a trait traditionally considered to be fixed.

3.2.6 Discerning sympatric categories of Blackcaps

In order to discern M, R and W birds (see Figure 7 below), we based on the fact that flight morphology in Blackcap is known to vary according to migratory behaviour (Fiedler 2005). Length of tail, wing, tarsus and wing pointedness of Blackcaps captured in Cocentaina during the whole year cycle were used to build discriminant functions, aimed to discern sympatric categories of birds: R from W and M from R. Given that morphological differences between fractions of the same breeding populations differing in migratory behaviour may be lacking (e.g. Fudickar and Partecke 2013), traces of stable isotope in claws and feathers of these two categories of birds were analysed in search of a discriminant factor. Previous to isotope analyses, tissue samples were cleansed and processed following standard methodologies and finally sent to a specialized laboratory (Agroisolab of Jülich, Germany) where the analyses were performed.

Overall, Chapter VI is dedicated to explore morphological and isotopic differences between Blackcaps differing in migratory behaviour, similarly to previous studies (Pérez-Tris et al. 1999, de la Hera et al. 2007 and 2012), but approaching a system in which three instead of two categories of birds are found sympatric.

4. Results and discussion: an overview

4.1 Wintering of trans-Saharan birds in Western Mediterranean

The compilation of data on the wintering of long-distance migrants north of the Sahara leaves no doubt: many individuals of several species spent their winter every year north of the desert. This result is evident in pure quantitative terms, given that more of the half out of the 80 considered species shows a great number of wintering cases (see Figure 1, Chapter I). The qualitative approach shows that in the last time window (2001-2006), 41 out of 80 species were present every year in moderate to high numbers (Chapter II), bringing us to the same conclusion.

Shortening of migration distances is an adaptive response largely observed in short and middle-distance migrants (van Vliet et al. 2009; Visser et al. 2009; Smallegange et al. 2010; Pulido and Berthold 2010; Heath et al. 2012), and was also expected to occur in long-distance migrants (Berthold 2002, Fiedler 2003, Coppack and Pulido 2004, Pulido 2007b). However, to the date, only sporadic, anecdotal episodes of wintering north of the Sahara were known (e.g. Berthold 2001, Sutherland 1998, Newton 2008). Thus, this finding

Figure 5
Various moments of the field work. A: a mist-net in a spring territory; B: ringing and measurement; C: a ringed Blackcap observed through the telescope; D: observation place; E: a moment of radio-tracking in winter: equipment is composed by receiver, antenna and headphones; F: male Blackcap with the transmitter mounted on the back. Photo: M.Morganti: A,C,D,F. E.Castoldi: B, E.

represents the first comprehensive description of the shortening of the migration distances in trans-Saharan birds covering a wide spatial and temporal scale.

4.2 Increasing of the wintering records in the time

The number of wintering birds showed a significant increase between 1969 and 2006 (Figure 1 in Chapter II and Table S2 in Chapter III), even accounting for the temporal autocorrelation, which is probably due to the increase of monitoring effort during the study period. This finding agrees with the hypothesis that wintering of trans-Saharan migrants north of the desert is an adaptive response to climate change. If the number of wintering records would not progressively increase, observations of wintering birds could merely represent the erratic presence of some individuals. This may be the case for some species which have numerically huge breeding populations in Europe and show some wintering records, which are, however, insignificant compared to the population size (e.g. Willow warbler *Phylloscopus trochilus* and Garden warbler *Sylvia borin*). Interestingly, neither population size nor population trend seemed to determine the probability of a species to establish wintering populations north of the Sahara (see Result 4.4 below and Chapter II).

4.3 Concentration of the wintering records in coastal wetlands

Both at the scale of Spain (Figure 2 and Table 2, Chapter I) and of the western European flyway (Figure S2, Chapter II) most of the wintering cases were concentrated in wetlands, where species that are not wetland specialists converge also during winter. This may be due to the year-round availably of many types of resources (fruits, insects etc.). Wetlands are a scarce and threatened environment in the world (Turner et al. 2000) and international conventions tend to protect these habitats (Ramsar, Natura 2000, "Birds" Directive 2009/147/EC). Thus, most of the areas defined here as hot-spots for wintering of trans-Saharan migrants have already benefited of some degree of protection under the Ramsar convention (www.ramsar.org) or the Natura 2000 European convention. However, this may not be the case for some wetlands that do not fulfil the traditional requirements (e.g. to host at least 20,000 wintering birds or the 1% of the individuals of a species are some criteria to be included in the Ramsar convention) to be included in these international conventions. Our results show that small wetlands, even environmentally degraded, may hold a great importance for species that have recently begun to spend the winter in these areas. The importance of these sites is likely to grow in the next years. The relevance that an area will have in the future under a climate change scenario should be taken into account in large-scale conservation policies. Thus, ultimately, the distribution of wintering events reported in Chapters I and II confirm the need of climate change-integrated conservation strategies ("CCS", Hannah et al 2002). Finally, data like the one presented here, may significantly support conservation policies directed to migratory species, given that helps to identify

new wintering areas, something strongly advocated by the Convention of Migratory Species (CMS) that in 2011 make a call for protecting this type of areas (see, UNEP/CMS Resolution 10.19: http://www.cms.int/bodies/COP/cop10/resoltions_adopted/10_19_climatechange_e.pdf).

4.4 Ecological characteristics that facilitate the establishment of wintering populations north of the Sahara

In Chapter II, many species-specific characteristics (see 3.1.4 above), as well as specific population trends, were tested as predictors in a model that, controlling for phylogeny, had as a response variable the probability of a species to establish wintering populations north of the Sahara. Five principal components were obtained from the PCA performed on species-specific characteristics: (PC1) Spring migration phenology, (PC2) Winter range extension, (PC3) Fall migration phenology, (PC4) Northern limit of breeding area and (PC5) Phenology of the end of the breeding period. These components were entered in the models and PC1 and PC2 emerged as the most important variables in the best model (Chapter II). Wider sub-Saharan wintering quarters and earlier dates of spring migration enhanced the probability that a species establish wintering populations north of the Sahara (Figure 6).

Species that migrate early spring may have a lower limit of thermal tolerance, allowing them to survive in the new wintering quarters of temperate latitudes. Moreover, these "early migrants" are the species that are supposedly exposed to the strongest selection for early arrivals. The amplitude of the traditional wintering ranges may be related to the ability of a species to spend the winter in a wider variety of environments, suggesting greater habitat plasticity (Thorup 2006). Similarly, wider wintering ranges may be associated to more plasticity in the physiological response to alterations in the photoperiod, which is a physiological prerequisite for adaptive changes in wintering latitudes (Coppack and Pulido 2004).

4.5 Different rate of establishment of wintering populations for passerines and non-passerines

Even if both passerines and non-passerines species showed a significant increase in the number of individuals wintering north of the Sahara during the last decades (Figure 1, Chapter II), this increase was significantly lower for passerines. Moreover, when looking at the specific data, it becomes clear that the increase among passerines is mostly due to a few species; basically swallows (*Hirundinidae*) and the Yellow wagtail (*Motacilla flava*) (see Figure 1 in Chapter I and Table S2 in Chapter III). Swallows and wagtails include species that segregate to winter in very differentiate regions of the globe (e.g. sub-Saharan Africa and Indian subcontinent)(Thorup 2006), thus suggesting greater ability to winter in new habitats (see 4.4). Sample sizes shown in Figure

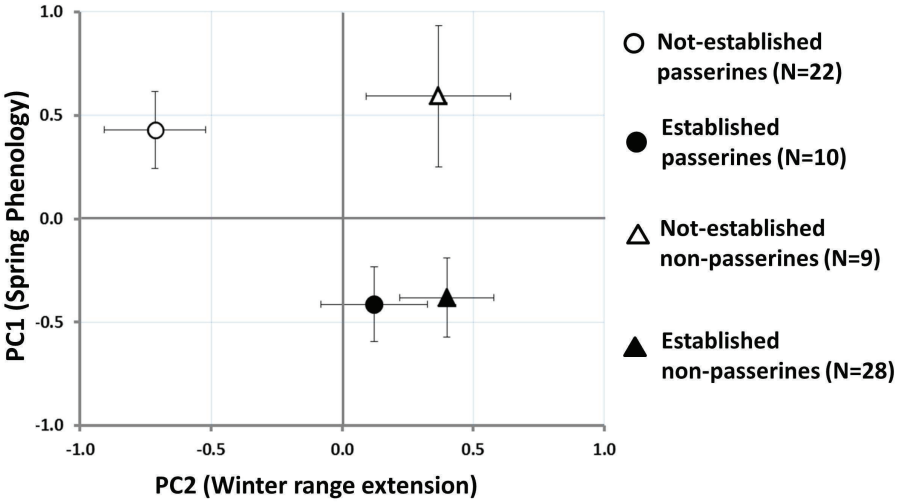


Figure 6

Mean values of the principal components related to spring phenology (PC1, Y axis) and winter range extension (PC2, X axis) for 69 species of European trans-Saharan migrants. Positive values indicate later spring phenology and higher migration distances. Species are divided in four groups discerning between passerines and non-passerines and between species that established stable wintering populations north of the Sahara ("established") and species that did not ("not-established"). Position of the dots indicates mean value of the group of species, standard error of mean is shown by whiskers. Figure 3 of Chapter II shows the same graph but drawing individual values of each species.

6 confirm the general pattern: while 28 over 37 species of non-passerines established wintering populations north of the Sahara, only 9 of the 32 passerines species did the same.

This finding confirms the general inertia of long-distance passerine migrants to change their migratory patterns (Widmer and Pulido 2005). Indeed, among all known cases of populations that changed migratory routes, only 8 out of 52 cases belonged to passerines (Newton 2008). Only recently, new studies on social migrants showed that constrains on adaptation of migratory habits can exist among non-passerines too. Spoonbills (*Platalea leucorodia*) and Flamingoes (*Phenicopterus roseus)* using the Western European flyway migrate during their whole life to the wintering site they learned during their first migration, even if survival probability is lower than in other (maybe nearer) sites (Lok et al. 2011and 2013, Sanz-Aguilar et al. 2012). This had been defined as a "cultural constrain" on adaptive changes of migratory patterns (Lok et al. 2013). Overall, distinction of passerines/non-passerines mainly covers two different control systems of migration: on the one side the strictly genetic controlled system typical of passerines

(Berthold and Querner 1981), and on the other the largely cultural and social determined system typical of non-passerines (Mueller et al. 2013). In terms of a quick adaptive response, the second is expected to be more efficient, given that it can largely rely on plasticity of migratory phenotype (see 1.3 above). Our results support this view, given that in the time scale of some decades, the latter showed a vast and huge adaptive response, while the first almost lack of it. Indeed, this result do not exclude that passerines can adapt, but this should happen at evolutionary time scale. Even if, at least among passerines, evolutionary changes can be quick (e.g. Pulido and Berthold 2010), rates of adaptation required to cope with climate change may be still too high for these species that may get extinct before to have time to adapt to it.

4.6 The role of temperature trends

The analyses of temperature trends in Europe in the last decades showed that for most of the species the number of wintering records north of the Sahara between 1969 and 2006 was not related to climate warming in any of the considered life phases and geographical areas (Chapter III). Thus, overall, no evidence was found that climate warming is directly responsible of the increasing of wintering population of trans-Saharan birds in the western Mediterranean.

This finding suggests that the role of temperature changes in the shortening of migration distances in European migratory birds needs to be revised, particularly considering that simple positive trends in temperature are not the only aspect of climate change. For example, we found that despite generalized climate warming (IPCC 2007) winter temperatures in Western Mediterranean did not increase at all between 1969 and 2006 (Figure 3 in Chapter III). However, warming is not just a matter of changes in average annual temperatures: unnoticed changes in some thresholds (e.g. 0°C) relevant for organisms (an issue poorly studied), could be the real key elements of climate warming. Additionally, a part from climate parameters, an important factor favouring the wintering of trans-Saharan migrants in Iberia in Morocco may be the increased availability of food during winter. This may have anthropogenic causes and enhances the survival probability for species able to feed on these resources. For example, residency in Iberian White Storks (*Ciconia ciconia*) may have been promoted by the use of refuse dumps and the spread of some invasive species, like the Red swamp crayfish *Proclambarus clarkii* (Máñez et al. 1994; Gordo & Sanz 2006; Zwarts et al. 2009). Similarly, the rapid microevolution of migration to new wintering sites in the United Kingdom and Ireland by Blackcaps from central-Europe may have been promoted by the spread of bird feeders in the area (Berthold et al 1992). Finally, the relevance of climatic trends and habitat changes in traditional sub-Saharan wintering quarters is possibly higher than expected in establish the large adaptive response of shortening of migration distance observed in Chapters I and II. Ecological conditions in sub-Saharan Africa have strong consequences on the habits of long-distance migrants both on the short time scale, thus affecting arrival

date (Tøttrup et al. 2012) or breeding date (Saino et al. 2004), as well as on the long-term time scale because determines population trends (Zwarts et al. 2009).
In particular, oscillation in Sahel rainfalls has a great importance on European populations of trans-Saharan migrants (Zwarts et al. 2009). Overall, it seems reasonable to suggest that worsening of ecological conditions in the traditional African wintering quarters favoured those individuals wintering elsewhere, but the importance of this factor needs to be further explored.

4.7 Continue shifting of wintering latitudes even once north of the Sahara

Wintering latitude of most of the species that have established wintering populations north of the Sahara showed a continuous northward shift at intra-Palearctic latitudes. This shifting both affects latitude of the centre of occurrence and of the northern edge of winter distribution (Chapter IV). Northward shifting of wintering quarters as a response of climate change is a well-known pattern among short-distance migrants from all over the world (La Sorte and Thompson 2007, MacLean et al. 2008, Visser et al. 2009, Heath et al. 2012, Lehikoinen et al. 2013). However, our result is the first evidence that the same pattern is found in long-distance migrants (but see Ambrosini et al. 2011). Furthermore, by linking our results with the ones of Ambrosini et al. (2011), the Barn swallow becomes the first species for which the full process has been described: i.e. progressive northward shifting of the traditional wintering quarters (Ambrosini et al. 2011), establishment of wintering population north of the Sahara (Chapter I and II), and continuous progressive northward shifting of the new wintering quarters (Chapter IV). Indeed, to be ideal the three steps would occur successively and not contemporarily as in the case of Barn swallow but this is possibly due to the fact that different populations of Barn swallows are at different steps of their adaptive process. An important implication of this general shifting of wintering areas within the Palearctic is that changes in traditional sub-Saharan wintering quarters are less likely to have played a major role in determining the observed pattern, giving that all happens at intra-Palearctic latitudes. Climate and land-use changes in Europe are the main candidate factors to explain this progressive shortening of migration distance at intra-Palearctic latitudes despite their role in determining the whole adaptive shortening of migration distances (from long to short-distance migrants) may have been not exclusive (see 4.6).

4.8 Complete moult in juvenile Blackcaps

Chapter V describes, for the first time, that in two different wild populations of Blackcaps a low proportion (about 1.6%) of first-year birds undertake an unusual complete plumage moult, which follows the adult pattern. Phenotypic variation in moult patterns is mainly due to genetic differences (Berthold and Querner 1982, Pulido and Coppack 2004, de la Hera et al. 2013), so that variation from the norm in moult-related features is likely to be

genetically determined. At least for one bird, which originated from the southern of the two studied populations, genetic determination of the complete moult was demonstrated by means of a common-garden experiment (see 3.2.5). In Chapter V, data from captive birds born in Cocentaina were merged with those from a long-term constant-effort ringing site in northern Spain (Garaio: 42° 54'N, 2° 32' W, province of Alava), where a low percentage of first-year Blackcaps was also detected to undertake a complete moult. Comparison of the two results suggests that the observed variance in moult pattern may be present in many wild populations. The difficulty to detect such a moult pattern further suggests that its frequency may be underestimated. We thus conclude that even well-studied life-history traits as moult patterns in a common bird as the Blackcap present undetected variance in its expression.

This study suggests that undetected variation in important traits may exist, which may fuel the adaptive potential of migratory birds. Interestingly, these findings were made in two populations that differ in their migratory behaviour, suggesting that the existing variation is not only maintained in partially migratory populations, where it is expected, but also in completely migratory populations.

4.9 Discrepancies between plumage morphology and behaviour

Individual capture-recapture histories demonstrate that, at least, part of the Blackcaps breeding in our study area of Cocentaina behaves as residents (Chapter VI). However, a previously published discriminant function developed to discern between migratory Blackcaps from central and northern Spain and sedentary Blackcaps from Gibraltar area (de la Hera et al. 2007), showed that flight morphology of our study population resembles the morphology of Spanish migratory blackcaps rather than of residents (Chapter VI).

The historical re-colonization of the central and northern Iberian Peninsula by Blackcaps that survived in the Gibraltar glacial refugia occurred by the northward expansion of originally migratory populations (Pérez-Tris et al. 2004). Blackcap populations in Eastern Spain are likely to have the same origin (Pérez-Tris et al. 2004). Therefore, we assume that our study population was originally fully migratory and only recently developed partial migration. Changes in the migratory condition of Blackcaps can be extremely rapid (see, Pulido and Berthold 2010). The occurrence of resident Blackcaps that retain "migratory appearance", as the ones described here, suggests that adaptive changes in morphology occur at lower rates than changes in migratory behaviour.

4.10 Morphologies of the two fraction of a partial-migrant population

Individual capture-recapture histories of Blackcaps from our study population suggest the occurrence of partial migratory behaviour (Figure 7). At the same time, the study area is also occupied every

year by large numbers of migratory Blackcaps from northern latitudes during the winter. Our study of the morphology of the three type of birds

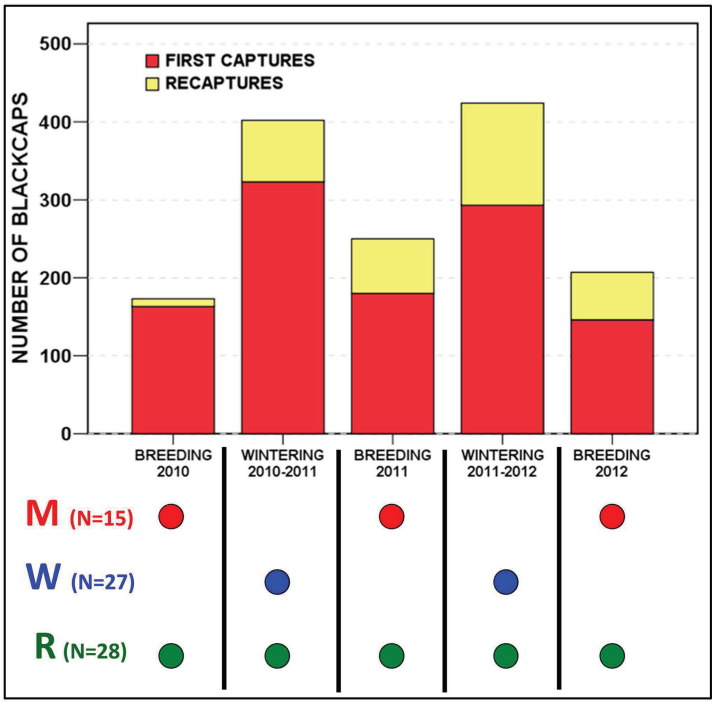


Figure 7

Total number of captures and recaptures during the five field seasons. Dots represent captures or re-sightings and show the pattern that individual histories had to match to be classified as northern wintering (W), local resident (R) or local migrant (M). 70 out of 1,054 captured Blackcaps were recaptured between different seasons and classified according to this scheme.

present in our study area [R,M,W: see Figure 7] confirm that flight morphology strongly differs between local breeders (R+M) and north-European Blackcaps (W), even taken into account that the studied population is not fully resident and more "migratory shaped" than Iberian blackcaps from further south (Chapter VI). This suggests that selective pressures shaping flight morphology in relation to migration distance are very strong. Therefore, we expected to find the same differences at the intra-population level between the resident and migratory fraction of the studied partially migratory population. However, this was not the case: migrants and residents from our study area were morphologically indistinguishable (Chapter VI). Analysis of isotopic signature in claws of birds collected in early reproductive season also failed in discerns between M and R birds.

These findings are coherent with a model of environmentally-driven partial-migration, in which individuals behave as migrant or resident depending

on intrinsic (sex, age) or extrinsic factors (e.g. food abundance). Moreover, a part of only migrate in some years but not in others, migrants may only move few kilometres away, further depleting the powerful of selective pressures eventually shaping morphological differences among migrants and residents.

4.11 Dominance relationships between resident and wintering sympatric Blackcaps

Given that morphological discriminant function permitted reliably identifying local and northern wintering Blackcaps (see 4.10), behavioural observations in winter permit to verify if variation in migratory behaviour is associated to variation in dominance. Resident Blackcaps were clearly dominant over wintering ones (Table 2 and Figure 4 in Chapter VII), even if the latter were generally bigger (Figure 2, Chapter VII). This result was obtained even if dominance score and body size were positively associated (Figure 3, Chapter VII), as it generally occurs among animals (Brown and Maurer 1986). Other factors as sex and experience possibly also contribute to determine the outcome of aggressive interactions (Table 2, Chapter VII), confirming general patterns found among birds (e.g. Cristol et al. 1990, Barluenga et al. 2000, Jahn et al. 2010b). A further factor that could have determined dominance status and not considered in our analyses, is prior residency effect (i.e. the probability of the owner of a territory to maintain it during a match), that can overcome the importance of sex age and body size in determine the output of aggressive interaction (Cristol et al. 1990).

4.12 Winter home ranges and habitat selection of resident and wintering Blackcaps

Using telemetry tracking, we showed that R and W birds settle down in winter home ranges that differ for their habitat composition, being the R ones more varied (Figure 5a, Chapter VII). However, habitat selection operated within home ranges makes that the two categories of birds spend a similar proportion of time in the same habitat types (Figure 5b Chapter VII). Results about habitat selection suggest that specific habitat categories (possibly olive groves for feeding and *Arundo donax* reedbeds for roosting) are of crucial importance for a successful wintering both for R and W birds. Thus, differences in composition of home ranges may be due to the fact that R maintain home ranges that include habitat typologies of low utility during winter but that will be determinant of territory quality during the following breeding season. Ultimately, this may lead the R birds to stay in home-ranges that are suboptimal in terms of winter needs and bring them to the (slightly) worst body conditions if compared to W conspecifics (Figure 2, Chapter VII). Finally, the pattern described by our results may solve the dichotomy observed in wintering Blackcaps in Gibraltar area, where R and W birds settle down in different environments (Pérez-Tris and Tellería 2002, de la Hera et al. 2012), but have the same diet (Tellería et al. 2013).

4.13 Occurrence of sex-mediated partial migration

The proportion of wintering migrants (W) relative to local resident (R) strongly differs between age and sex classes, being highest in adult females (see Table 1, Chapter VII). Females are also subordinate to males (Figure 4, Chapter VII). These two findings suggest the occurrence of partial migration in the local breeding population, in which females are more likely to migrate. Differences in the migratory behaviour between sexes are a common pattern among short-distance migrants (Newton 2008). Obligate female-biased partial migration had been recently described in Blackbirds (*Turdus merula)* from southern Germany (Fudickar et al. 2013). Different susceptivity of male Teals (*Anas crecca*) compared to females to the harshness of weather in northern Europe cause differential migration in between sex classes (Guillemain et al. 2005), determining an ecologically-mediated partial-migration of northern European populations of this species.

Interestingly, proportions of W and R birds among first-year birds are less extreme than among adults: R birds are more common among first-year birds (Table 1, Chapter VII). Thus, the overall evidence suggests a pattern in which adult females have the highest propensity to migrate, while juveniles of both sexes are more likely to be resident. This may be due to the fact that while adults need to maintain a territory during winter, juveniles will behave as subordinates in any site they would migrate. Therefore, to them the best strategy is to be resident, which, at least, saves the cost of migration. This unusual behaviour partially reflect what has been observed in tropical partial-migratory systems (Boyle 2008, Jahn et al. 2010b), and will probably found in other migratory bird species.

5. Future outlooks

This thesis gives some insight on the capacity of migratory birds to adapt to global change, answering some crucial questions but also opening new topics, which will need further investigation.

One of these topics regards the origin of the trans-Saharan birds observed wintering north of the Sahara. Are they southern European breeders that became residents? Are they northern European birds that are shortening their migration distances? Or are they a mix of both? Theoretical models shown in the Introduction suggest that most of the cases should involve northern European populations. The continuous shifting of the wintering latitude described in Chapter IV, joined with the evidences that this shift was not due to amelioration of winter climate in Iberia (Chapter III) support the hypothesis of a northern European origin of the new wintering populations, because if the Iberian birds became resident such pattern would not to be expected if not supposing that a parallel northward

shift of the breeding range of these populations also occurred. Empirical results about the breeding origin of the wintering birds would allow refining the model on the adaptive shortening of migration distances. A possible way to obtain this information is offered by isotopic signature: δD of feathers moulted at the breeding quarters of birds captured in winter north of the Sahara can easily assess the origin of the bird, especially if compared with δD of birds of known origin. A perfect model species for such a study would be the Little bittern (*Ixobrychus minutus*), that now have well established wintering populations north of the Sahara and aggregate in wetlands also in winter, enhancing capture probability.

Another question that needs to be explored regards the hypothesis that the progressive shortening of migration distance is an adaptive process, which facilitates an advancement of arrivals at the breeding grounds. This predicts that populations that are wintering north of the Sahara have succeeded in advancing their arrival dates. However, this test had never been done. The main difficulty is that this test would need to be done at a population scale, thus implying the knowledge of the migratory movements of a representative part of the population, something that may be possible in the near future thanks to the new tracking technologies, but that nowadays is impossible especially on small-sized birds. However, a less precise but much easier approach would be to use the whole species instead of the population as raw data. In such a test, a simple positive correlation between rate of advancement of arrival date and rate of growth of the wintering populations would indicate that the adaptive shortening of migration distance has facilitated the advancement of arrival dates, and this may be the driving selective factor in these species.

Another point that needs to be further investigated relates to the climatic and environmental patterns that predicts the occurrence of wintering events (e.g. rain patterns, max and min temperatures). Based on our data it would be straightforward to extract those variables that best explain the distribution of wintering events of trans-Saharan migrants north of the Sahara and elaborate a spatial model that would allow predicting the current and future distribution of these events over the entire Mediterranean. The results presented in the thesis (Chapter III) show that the analysis of single climatic parameters does not satisfactory explain the emergence of new wintering habits north of the Sahara, calling for the use of integrated spatial environmental-climate modelling. Moreover, such a model would be a useful conservation tool, which would allow integrating effects of climate change on the designation of protection networks.

6. Conclusions

6.1 A general reduction in migration distances occurred in European trans-Saharan migrants in the last decades and is still on-going at intra-Palearctic latitudes.

Establishment of wintering populations of many species of long-distance migrants north of the Sahara along the western European flyway emerged from data compiled in this thesis. During the last decades, the number of species and individuals has progressively increased in the new wintering quarters. A northward shift of the new wintering areas is continuing among populations established north of the Sahara. The whole process is consistent with predictions on the adaptive response that may help migratory birds to cope with the new selective regimes imposed by climate change in the northern hemisphere, which are mainly characterized by favouring earlier arrival at the breeding areas.

6.2 Establishment of wintering populations north of the Sahara is more likely for species that have wide wintering ranges and return to their European breeding sites early in the spring.

Species used to winter in a large variety of habitats and migrate back to Europe early in the seasons are possibly pre-adapted to cope with relatively unfavourable conditions both during wintering period and during migration, so that establish wintering populations at northern latitude with greater probability. Given the speed to which global change is occurring, and the rate to which selective pressures for earlier arrival at the breeding quarters are running, only species with flexible migration schedule and great tolerance to environmental conditions may be able to develop the adequate adaptive response, as wintering in the Mediterranean basin in this case.

6.3 Establishment of wintering populations north of the Sahara is generally constrained among passerines species.

The coarse distinction between passerines and non-passerines species remains a very effective tool to describe the lack of adaptive response in a vast number of long-distance migrants, which almost exclusively belong to the order *Passeriformes*. Of course, this difference is thought to reflect differences in the control of migration, considered to be strictly genetic (and less flexible) in most of the passerines, while more environmentally and social-mediated in non-passerines. The review of the few passerines species that established wintering populations north of the Sahara confirmed this hypothesis, given that they all migrate in groups and have highly social habits.

6.4 Recent temperature trends in Europe are not linked with the establishment of long-distance migrants north of the Sahara.

Changes in other climatic variables, as well as in land use may have played a major role in improving the suitability

of north-Saharan regions as new wintering quarters for trans-Saharan migrants. At the same time, worsening of ecological conditions in traditional wintering quarters probably contributed to reinforce selection favouring shorter migration distances.

6.5 Undetected variation in genetically determined traits occurs in wild bird populations and possibly contributes to their adaptive potential.

Even in a well-studied passerine as the Blackcap, our knowledge of the extent of the factors that fuel adaptive potential is limited, as shown by the occurrence of previously undetected genetic variation in moult patterns. The fact that this was found in two populations differing in migratory habits (fully migrant and partial-migrant), suggest that undetected phenotypic variation may be commonly present in wild bird population. Eventually, this may be regarded as a stock of adaptive genetic variation that is generally hard to detect.

6.6 Changes in flight morphology mediated by natural selection occur at a slower rate than changes in migratory behaviour and do not result in different morphotypes in residents and migrants in a partially migratory population.

Occurrence of "migrant-shaped" resident Blackcaps suggests that populations that presumably became resident recently, need longer time to adapt their morphology to the new behavioural condition. This may indicate that the strength of selection shaping flight morphology is not intense, which is also supported by the fact that residents and migrants of the same breeding population are morphologically indistinguishable. However, if partial migration is environmentally determined, different morphologies would not emerge, given that selective pressures on morphologies would fluctuate on a yearly scale.

6.7 Energetic costs to behave as resident and inability of migrant individuals to gain territories held by residents contribute to maintain the great variability of migratory habits in the Blackcap.

In sympatric wintering grounds, resident birds are involved in aggressive interactions with migratory conspecifics and maintain home-ranges with more varied habitats, although they use the same resources as migrants, which settle in home-ranges that better reflect winter needs. For local breeders, maintaining their territory throughout the year may be advantageous in terms of fitness. However, this behaviour is energetically costly and only some birds, adult males in particular, may be in the condition to undertake it. Together, these factors probably contribute to maintain the wide variety of migratory habits observed in Blackcaps. Given that variability fuels adaptive potential, these mechanisms ultimately maintain high the potential for population of this species to cope with climate change.

Section I

Shortening of migration distance in European trans-Saharan migrants

A group of Barn swallows (Hirundo rustica) that overfly a snowy field. This paradoxical picture could become reality in the coming years.

Background paint by Steave Greaves www.steavegreaves.com, and Barn swallows paint by Juan Varela www.juanvarela.it . Both artists kindly allowed the use of their artworks.

CHAPTER I

Wintering of trans-Saharan birds in Spain

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1. Introduction

Bird migration strategies have evolved as an adaptive response to seasonal fluctuations in resource abundance (Alerstam et al. 2003). In this sense, long-distance migration allows birds to profit of environmental conditions of maximum productivity all year-round (i.e. during spring-summer at temperate-boreal latitudes in the Holarctic and during winter at tropical latitudes). Migration strategies and especially contemporary migratory routes of European migratory birds have evolved after the last glaciation, but they are dynamic and may vary in response to expansions and displacements of breeding and wintering areas, establishment of new winter quarters, local extinctions and other factors (Sutherland 1998, Newton 2008). These processes have occurred repeatedly and independently in different species, so that they must be taken into account to correctly interpret the Palaeartic-African migration system as it is nowadays (Salewski and Bruderer 2007, Newton 2008). There is an intense open debate about which selective pressures are at the origin of the evolution of long-distance migratory strategies, (Alertsam et al. 2003). It is still discussed whether long-distance migrants descend from tropical ancestors that became migratory while colonizing northern latitude or by northern ancestors that developed south-directed migratory movements. However, there is a large consensus that climate changes had a crucial role in shaping migratory strategies (Salewski and Bruderer 2007, Newton 2008). In particular, current migratory routes of many species from Europe and North America seem to originate from re-colonization of northern latitude by residual population hosted in southern glacial refugia, after the end of the last glaciation period about 10.000 years ago (Newton 2008).In recent decades, the Palaearctic-African migratory system has been changing in response to rapid global climate change, which is mainly characterized by a marked increase in spring temperatures in the Northern Hemisphere. This warming causes an advancement of phenology of spring events, such as the unfolding of leaves and flowers and the appearance of caterpillars and insects, on which the reproductive success of many birds depend (Cox 2001, Parmesan 2006, Visser et al 2009). Therefore, migratory patterns and arrival date at the breeding grounds could become maladapted to the new environmental conditions

Currently, many migratory birds arrive too late to take advantage of the bonanza of feeding resources, which are available only during a short time window in spring (Both and Visser 2001, Saino et al. 2011). This phenological mismatch is thought to be the main selective pressure that promoted the most apparent shift observed in the migratory habits of birds in the last three decades: the advancement of migration and arrival dates (Lehikohinen et al. 2004, Cox 2010, Knudsen et al. 2011). Other changes in the phenology of birds' habits have also

been observed, as the advancement of reproduction (Crick and Sparks 1999), that demonstrate that birds are virtually able to quickly adapt to the new environmental conditions.

Current climate change forces birds to adjust their life cycles to the new demands (selective pressures), although it may happen that the advancement of migration and arrival dates are not enough to compensate for the actual advancement of spring events. Actually, it has been demonstrated that European species that do not advance enough their life cycles are suffering population declines (Møller et al. 2008, Saino et al. 2011), once again showing that strong selective pressures are favouring an advancement of arrival dates.

So, which are the possible mechanisms through which a migratory bird could achieve this advancement? Three possible ways had been described (Coppack and Both 2002, Pulido 2007b): (1) the advancement of the onset of migration; (2) increasing the speed of migration, and (3) the reduction of migratory distance. The last option confers further advantages, like significantly reducing the cost of migration and allowing an advancement of physiological development in response to exposure of photoperiods from northern latitudes (Coppack and Pulido 2004). Thus, it is expected that a reduction of migratory distances will allow migratory birds to achieve an earlier arrival dates. Consequently, climate change is favouring sedentary and partial migration behaviours more than long-distance migrations (Berthold 2001). Indeed, a reduction of migration distances in short and middle-distance migratory birds has been already observed both in Europe and North America (La Sorte et al. 2007, Visser et al. 2008).

Concerning the Palaearctic-African migratory system, it is thus to be expected that long-distance migrants winter progressively at northern latitudes, obtaining a special benefit in overwintering north of the largest ecological barrier that cross in their migratory journeys: the Sahara. The Mediterranean basin is the wintering ground of many species of intra-European migratory birds, and the peninsulas of Iberia, Italy and Greece is the main wintering area for these species (Handrinos and Akriotis 1997, Cramp and Simmons 1998, Berthold 2001, Spina and Volponi 2008, SEO/Birdlife 2012). Therefore, it is within these peninsulas where one may expect to find evidences for the shortening of migratory distance of birds that normally overwinter in sub-Saharan Africa.

There is some anecdotal evidence that birds are able to make this shortcut of their migratory journey (Sutherland 1998, Berthold 2001, Newton 2008). However, up to now, very few studies have demonstrated a direct link between phenological changes and establishment of new wintering quarters (Knudsen et al. 2011). A recent study demonstrated an on-going evolution towards a reduction of the migratory activity in the last 30 years in wild Blackcap (*Sylvia atricapilla*) populations from southern Germany, and this decrease appears to be consistent with an adaptive response to

climate change (Pulido and Berthold 2010).

Therefore, in the context of an Atlas of wintering birds in Spain it was particularly interesting to specifically study the winter-presence of trans-Saharan species, with the aim of elucidating whether changes in their migratory pattern in the Iberian Peninsula are already a fact. A proper approach to this problem requires a database including a time and geographic scale as wide as possible. Luckily, to build such a database is possible, at least for Spain. The long tradition of interest in birds in this country is reflected in the foundation of the Spanish Ornithological Society (Sociedad Española de Ornitología SEO-BirdLife) in 1954. Few years later, in 1965, the Doñana Biological Station was founded, although not born as an institution exclusively dedicated to birds, it traditionally puts a great research effort on orhnithological research. Finally, in the following decade two of the other major ornithological societies of Spain were founded: the Balearic Group of Ornithology and Defense of Nature (GOB, 1973) and the Catalan Institute of Ornithology (ICO, 1975). Since the 1960ies the number of scientists and amateurs who devote their activities to birds has been increasing exponentially. To have an idea of the order of magnitude of this increment one can look at the number of members of SEO-BirdLife: from the 6 founders in 1954 it arise to the symbolic threshold of 1.000 in 1985, then touching the 12.000 in 2011 (SEO-BirdLife data). This tradition of interest in birds means that there is an enormous amount of information on the presence and distribution of birds that have been collected over a wide time window and over the whole territory of Spain.

We present here a summary of the wintering episodes of 80 trans-Saharan bird species, with the aim of describing the current situation and trace a baseline for future comparisons. Data presented here cover a time window spanning from the oldest data that we found until winter 2007-2008, and gives the opportunity to qualitatively compare the unsystematically collected "historical" data with the ones collected by standard methodologies during the work of this Atlas (sampling period of the Atlas: winters 2007-2010). We also included data from the Spanish ringing database concerning winter captures of the studied species.

2. Methods

We gathered all the published information about the winter presence in mainland Spain and Balearic Islands, starting from the publications available at the ornithological library of SEO-Birdlife in Madrid or published on the network or finally ordered directly to the authors. We consulted more than 400 publications and found useful information in 295 of these. We

considered 80 species of trans-Saharan migratory birds spanning across the whole phylogenetic range (Table 1). Species were chosen for their ecological and behavioural characteristics, trying to include those species that traditionally completely winter south of the Sahara. We decided not to consider species for which it was impossible to collect enough data to obtain a representative picture of their wintering situation. Therefore, we finally excluded species whose effective numbers in winter grew very large years ago (e.g. the White Stork that commonly winters in Spain from the '80s. Molina and del Moral 2005).

To approach the problem of variation in the detectability among species, we decided to include for same set of species all data of birds ringed between October and February. The Department for Migratory Species of the Spanish Ministry of Environment (MARM) provided ringing data for the period between 1952 and 2009 - a total of 27,300 records.

To reduce the possibility of erroneously counting an early or late migrant as a wintering individual, we established species-specific time-windows, which allowed us to identify likely wintering events (shown in Table 1). These windows were based on general migration phenology across Europe from Cramp and Simmons (1998) and adjusted to the migration date across the strait of Gibraltar (Bernis 1980, Tellería 1981, Finlayson 1992).

3. Results

Out of 10,006 collected records, 3,942 were selected following the criteria described above and considered as true wintering events. Most (59.8%) of these reports refer to observations of a single wintering individual, and 90.3% refer to observation of less than 10 individuals. However, some record refers to a large number of individuals (max: 1,249 Curlew sandpiper *Calidris ferruginea* observed in January 2008 during the winter bird survey in Doñana), so that the total amount of observed wintering individuals raises to 36,447. With 6,862 individuals, the Night heron *Nycticorax nycticorax* is the most numerous species, accounting alone for the 18.8% of the total observed individuals. The top species in term of number of records is the Booted eagle *Aquila pennatus* with 457 observations, 11.6% of the total. All the 80 species were observed in winter, although two species yielded only one observation each: the Grasshopper warbler *Locustella naevia* and the Wood warbler *Phylloscopus sibiliatrix*, both scarce migrant across Spain. Among passerines, only swallows (*Hirundinidae*) and the Yellow wagtail *Motacilla flava* have a significant number of wintering observations. Figure 1 summarizes information on the number of records collected for each species; data derived from visual observations and from ringing are marked in different colours.

Observations belong to 1,058 different localities, distributed all over Spain (except Canary Islands for which data were not collected, see Figure 2). The highest density of observations lies in the Eastern Mediterranean region, being the provinces of the Balearics, Alicante and Sevilla the most important ones (about 400 wintering events each). Four coastal provinces follow in terms of importance yielding between 200 and 300 events each. Each of the 48 provinces considered hosted at least one wintering episode, being Soria and Guadalajara the negative record with only 1 observation each.

The localities with the highest number of wintering events are coastal wetlands of varied size, as the one at the mouth of the River Guadalhorce in Málaga that with its reduced size of 100 ha collected 140 wintering events. Many of the localities with observations are located next to each other and concentrated in ecologically homogeneous environments, so that they can be considered as one single, large site (e.g. the area called "Guadalquivir Marshes – Doñana" includes information from 60 localities). Following this aggregation criteria, we have listed in Table 2 the first 10 sites in terms of number of observations collected. Overall, localities listed from in this table comprise 1,726 observations (43.78% of the total number of collected records).

4. Discussion

The review of wintering events of trans-Saharan species in Spain proves that the phenomenon is not mere anecdotal, being observed every year about 50 species.

Interestingly, during the sampling period of the Atlas (2007-2010) almost all the species of trans-Saharan migrants considered were observed. Only those species, which are normally very rare in the Iberian Peninsula and for which wintering records were hardly found during the complete study period, were were not observed during that period (Figure 1). This observation lead to the conclusion that (1) the dataset based on anecdotal information is reliable and representative of the real situation, and that (2) the species that were observed in the short time window considered by this Wintering Atlas are likely to have well established wintering populations. Otherwise, one would expect larger discrepancies between the list of species observed till 2007 and the ones observed in the following years. Figure 1 reveals that the majority of wintering cases belongs to species of medium to large size: a set of species that could be aggregated under the phylogenetically heterogeneous group of "*non-passerines*". This group of birds, contrary to the "*passerines"*, seems to have a greater ability to adapt to the new conditions imposed by climate change. In accord with this finding, only 8 out of 52 cases of species that changed migratory patterns reviewed by Newton (2008) were passerines.

Table 1

Systematic list of the considered species and specific time window in which a record were considered as a true wintering episode (window based on: Bernis 1980, Tellería 1981, Cramp and Simmons 1998, Finlaynson 1992). Shaded boxes show months considered as wintering period. Half shaded boxes indicate that time window close the 15th of that month.

	SPECIES	NOV	DIC	ENE	FEB		SPECIES	NOV	DIC	ENE	FEB
1	*Anas querquedula*					41	*Apus melba*				
2	*Ixobrychus minutus*					42	*Merops apiaster*				
3	*Nycticorax nycticorax*					43	*Coracias garrulus*				
4	*Ardeola ralloides*					44	*Calandrella brachydactyla*				
5	*Ardea purpurea*					45	*Riparia riparia*				
6	*Ciconia nigra*					46	*Hirundo rustica*				
7	*Pernis apivorus*					47	*Hirundo daurica*				
8	*Milvus migrans*					48	*Delichon urbica*				
9	*Neophron percnopterus*					49	*Anthus campestris*				
10	*Circaetus gallicus*					50	*Anthus trivialis*				
11	*Circus pygargus*					51	*Anthus cervinus*				
12	*Hieraaetus pennatus*					52	*Motacilla flava*				
13	*Pandion haliaetus*					53	*Cercotrichas galactotes*				
14	*Falco naumanni*					54	*Luscinia megarhynchos*				
15	*Falco vespertinus*					55	*Phoenicurus phoenicurus*				
16	*Falco subbuteo*					56	*Saxicola rubetra*				
17	*Falco eleonorae*					57	*Oenanthe oenanthe*				
18	*Crex crex*					58	*Oenanthe hispanica*				
19	*Glareola pratincola*					59	*Monticola saxatilis*				
20	*Charadrius dubius*					60	*Locustella naevia*				
21	*Calidris ferruginea*					61	*Locustella luscinioides*				
22	*Numenius phaeopus*					62	*Acrocephalus paludicola*				
23	*Tringa stagnatilis*					63	*Acrocephalus schoenobaenus*				
24	*Tringa nebularia*					64	*Acrocephalus scirpaceus*				
25	*Tringa glareola*					65	*Acrocephalus arundinaceus*				
26	*Sterna nilotica*					66	*Hippolais polyglotta*				
27	*Sterna hirundo*					67	*Sylvia cantillans*				
28	*Sterna paradisaea*					68	*Sylvia hortensis*				
29	*Sterna albifrons*					69	*Sylvia communis*				
30	*Chlidonias hybrida*					70	*Sylvia borin*				
31	*Chlidonias niger*					71	*Phylloscopus bonelli*				
32	*Chlidonias leucopterus*					72	*Phylloscopus sibilatrix*				
33	*Streptopelia turtur*					73	*Phylloscopus trochilus*				
34	*Clamator glandarius*					74	*Muscicapa striata*				
35	*Cuculus canorus*					75	*Ficedula hypoleuca*				
36	*Otus scops*					76	*Oriolus oriolus*				
37	*Caprimulgus europaeus*					77	*Lanius collurio*				
38	*Caprimulgus ruficollis*					78	*Lanius minor*				
39	*Apus apus*					79	*Lanius senator*				
40	*Apus pallidus*					80	*Emberiza hortulana*				

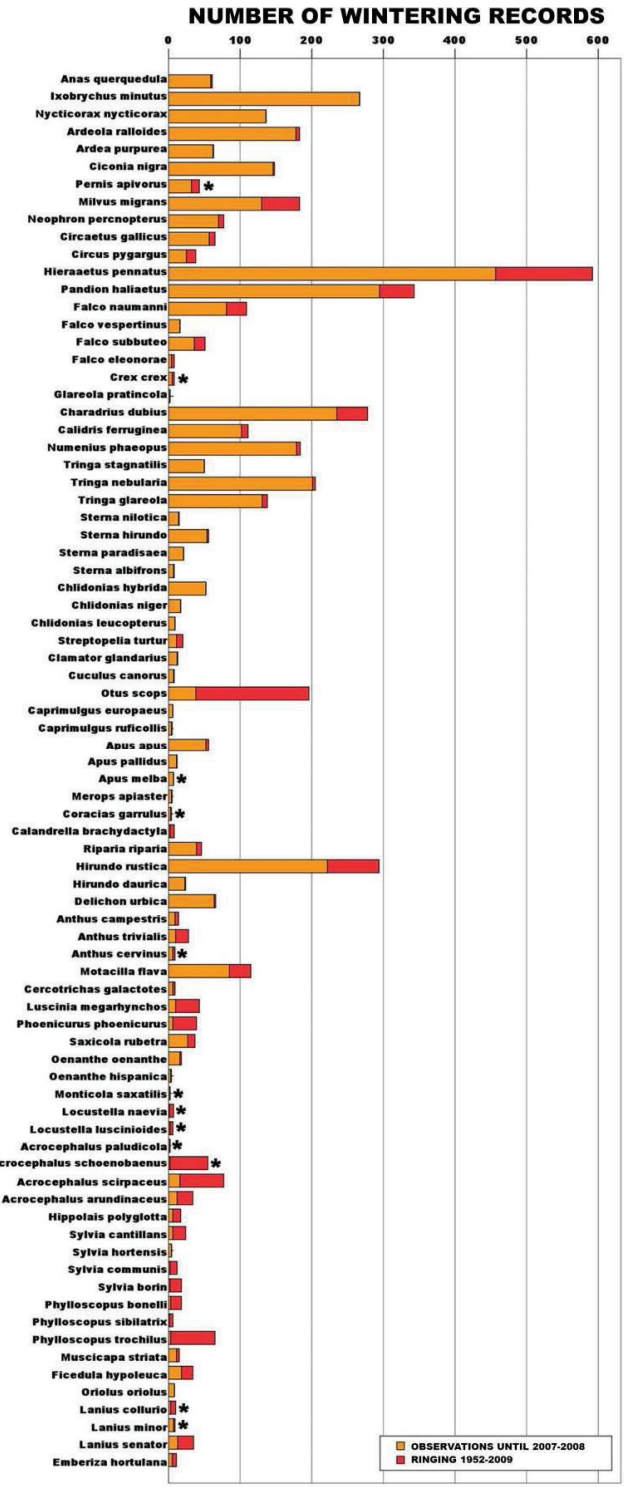

Figure 1

Number of wintering records of trans-Saharan species in Spain until winter 2007-2008.

These data cumulate visual observations (orange bars) from birds captured in ringing sessions (in red).

Stars indicate species that were <u>not</u> observed as winterers during the three years of sampling of the Atlas of birds wintering in Spain (SEO/BirdLife 2012).

Figure 2

Distribution among Spanish provinces (Canary Islands excluded) of wintering records of trans-Saharan birds until winter 2007-2008. Each record can refer to one or more wintering individuals.

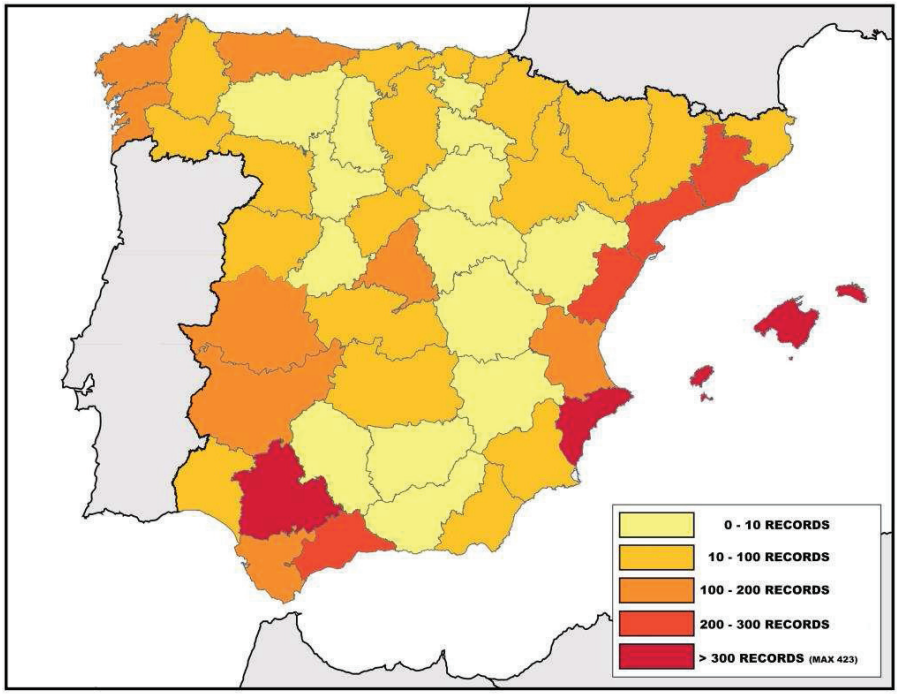

Table 2

List of the first ten localities for number of wintering records. The list includes precise localities or areas including group of nearby localities.

Area or locality	Region	Records
South-Alicante coastal marshlands	Valencian	342
Guadalquivir marshes - Doñana	Andalusia	338
Coastal marshlands of Valencia and Castellón	Valencian	231
Mouth of Ebro river area, Tarragona	Catalonia	159
Mouth of Guadalhorce River, Málaga	Andalusia	140
Albufera de Mallorca and surroundings	Balearic Islands	134
Western Galician Coast	Galicia	130
Gibraltar Strait area	Andalusia	111
Mouth of Llobregat river, Barcelona	Catalonia	91
Natural park of Aiguamolls de l'Empordá	Catalonia	50

A further exploration of this difference in the flexibility of migratory strategies and its relation to species-specific ecological, phylogenetical and biogeographic factors would shed light on the adaptive capacity of migratory birds facing climate change, ultimately providing guidelines for more effective conservation measures.

The geographical distribution of wintering events (Table 2 and Figure 2) corroborates the crucial role of the Mediterranean coast as wintering area for migratory birds within the European migratory system. This is a good argument to encourage a strong monitoring of these sites, and to achieve a level of protection for the areas that are not yet protected. These areas will become increasingly important as migratory patterns of European birds change. An example of the enormous importance of these areas for bird conservation is the case of the mouth of Guadalhorce River in Málaga (Table 2). This small and highly anthropized area is the only coastal wetland area in a radius of 300 km, and, therefore, regularly hosts a large number of wintering trans-Saharan migrants.

Finally, we need to consider that the database on which this work is based may be significantly biased if used to explore the progressive increase in the number of wintering cases. This is due to the fact that sampling effort (mainly given by amateurs' observations) has increased exponentially in the considered time period. Systematically collected data as done in this Atlas do not suffer such biases and if repeated within ten or fifteen years, they could reliably document tendencies for increasing wintering numbers of trans-Saharan birds in Spain.

5. Conclusions and future perspectives

The observation of trans-Saharan species wintering in Europe is extremely interesting for elucidating the effects of climate change, and therefore it should deserve growing attention in the future. A first step to improve the work presented here would be to expand the dataset to include data from Portugal and Morocco, to fully explore latitudinal patterns and the establishment of new wintering quarters along this along the Afro-European axis. Moreover, it would be extremely interesting to expand the surveyed area to the two other large Mediterranean peninsulas. The Atlas of Birds Wintering in Italy, for which monitoring started in 2012, will surely shed more light on this phenomenon. Finally, we want to point out that this work is a further confirmation of how valuable and useful the data collected and reported by thousands of amateurs all around Europe and the world may be. On the other hand, we invite scientist to dedicate more attention to this kind of data. The quality and usefulness of data collected by amateurs could significantly increase if collected within a coordinated and well-designed scientific framework. In this sense, the realization of this Atlas is a wonderful example of how scientists and amateurs can work together.

CHAPTER II

Rapid establishment of long-distance migratory birds north of the Sahara in winter

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Unpublished manuscript.

Abstract

Recent climatic alterations have caused profound changes in the migratory behavior of many bird species. Yet, it is unclear why some species have shown an adaptive response and others have failed to do so. To address this question, we studied shortening of migratory distances of 80 European trans-Saharan migrants. We show that wintering north of the Sahara has strongly increased over the last 40 years, predominantly in non-passerine species. This northward shift in wintering range may have contributed to the advancement of migration in these species, thereby facilitating the adjustment to phenological changes in their breeding areas. Species with a rigid control of migration, as found in most passerines, and a narrow range of ecological tolerance have failed to shorten migration distance, which will make them particularly vulnerable to climate change.

1. Introduction

Global change is one of the major threats to current biodiversity (Thomas et al. 2004, Bellard et al. 2012). Whether a species will survive or go extinct will largely depend on its potential to appropriately respond to rapid environmental changes (Parmesan 2006, Visser 2008). Migratory species are particularly vulnerable, because they have to cope with changes in the different areas in which they temporary live, which may compromise their adaptive response in each area (Robinson et al. 2009). Adaptive responses strongly differ among migratory species, though its causes are largely unknown (Berthold 1996). It has been hypothesized that the impact of global change is particularly severe in those species which travel the longest distances. In birds, these long-distance migrants are characterized by possessing a rigid endogenous control of migration (Pulido and Widmer 2005), which may result in reduced phenotypic variation in migratory behaviour (Both and Visser 2001, Pulido 2011). Low flexibility in migration has been proposed as a potential cause of phenological mismatch, reflecting low potential for adjustment to recent climate change (Coppack and Both 2002, Both et al. 2006), which may be an important cause of recent population declines in long-distance migrants (Berthold 2001, Møller et al. 2008, Saino et al. 2011).

Migratory birds could improve this situation by shifting their wintering areas to the north (Berthold 2001, Newton 2008). In this way, they could profit from reduced costs of migration, better information of conditions on the breeding grounds and from a physiological advancement of migration in spring and reproduction (Coppack and Pulido 2004, La Sorte and Thompson 2007, Heath et al. 2012). This shortening of migration distance has been proposed as an immediate and effective response of migratory birds to climate change (Visser et al. 2009). A northward shift of wintering areas has been demonstrated recently in short- and middle-distance migrants in Europe and North America (La Sorte and Thompson 2007, Visser et al. 2009, Pulido and Berthold 2010, Lehikoinen et al. 2013), but not in long-distance migrants. It is unclear whether this reflects the incapability of long-distance migrants to respond by this mechanism, or if it is an artefact caused by the low density of observers in the traditional wintering areas of these species, i.e. Africa and South America. Anecdotal observations of trans-Saharan migrants reported wintering in southern Europe (Berthold 2001, Newton 2008) and winter range shifts detected in the barn swallow (Ambrosini et al. 2011) may indicate that long-distance migrants can shift their wintering areas northwards, yet the extent and importance of these changes in migration are currently unknown.

Here, we studied the shortening of migration distance in long-distance migratory birds to assess their potential to adjust to recent climate change, and to identify the causes of among-species differences in adaptive response.

2. Methods

2.1 Data of Wintering Records

We created a database of winter observations of 80 European trans-Saharan migratory bird species in the Western Mediterranean Region (list in Table 1, Chapter I). Species were selected if they migrate along the western European flyway (i.e. the Iberian Peninsula, Newton 2008), and if by 1970 they wintered exclusively in areas south of the Saharan desert. We systematically searched all ornithological journals, including reports by local and regional ringing groups, and books, which regularly publish rare winter observations of wintering trans-Saharan migrants in the Iberian Peninsula and Morocco. The bibliographic search was conducted between 2008 and 2010. In 363 bibliographic titles (listed in Annex I at the end of the volume) we found relevant information and extracted a total of 9,981 records of our selected species for the months of November-February from 1866 to 2010. For the analyses, we used only the data for the period 1969-2006, since relevant publications were rare before 1969 and information after 2006 was incomplete, because of publishing delays. For each entry, we extracted the following information: site, date, number of birds and, when available, sex and age of the bird. We distinguished three types of records: (1) birds captured during ringing, (2) observations of individuals in the wild, (3) birds found dead. Sites were georeferenced by latitude and longitude. Observations from sites in Morocco south of 27^{o}N, i.e. the northern limit of the Sahara desert, were not considered.

For each species we defined a specific wintering period considering its migration dates across the Strait of Gibraltar (see Table 1 in Chapter I). Observations made outside this time window, records of dead birds and records, which according to the authors could include very late or very early migrants, were excluded. The database used in our analyses comprised 5,771 records.

2.2 Analysis of temporal trends in the number of wintering observations and in the number of individuals per observations

We estimated the effect of "year" on the number of wintering records of trans-Saharan birds, we log-transformed our response variable (i.e. number of wintering records/year) to achieve normality. We then fitted General Least Square (GLS) models with year as predictor and an autoregressive term of order 1 to account for temporal auto-correlation of data (Zuur et al. 2009). We tested more complex autoregressive structures with second and third order terms, but none of them was statistically significant ($p > 0.09$). Models were run with the nlme package of R software (Pinheiro et al. 2012).

In addition, we analysed trends in the yearly mean number of individuals per observations. This variable is insensitive to variation in observation effort, but may be sensitive to differences in territoriality and gregariousness of a species. Mean number of individuals was calculated for each species and year and square-root transformed prior to analyses to achieve normality. GLS models

were fitted as for number of wintering records variable. In addition, we fitted GLS models for each species separately and analyzed the distribution of the coefficients for the effect "year" for both dependent variables.

2.3 Qualitative assessment of the wintering status of species

With the aim to obtain a more robust measure of species presence in winter that could be used as an indicator of establishment of populations, we defined an index of wintering status for each species. Considering the relative abundance of a species compared to other species, partially corrects for the variance in observer effort, while the regularity of a species is a variable that is largely independent of its detectability. We calculated this index by transforming our records into four categories related to the number and the regularity of observations: anecdotal observations (status 1), few irregular observations (status 2), small to moderate number of regular observations (status 3), moderate to large number of regular observations (status 4). Wintering status was determined by considering the occurrence and abundance of species records in the study area during the winter as follows. First, the study period was subdivided into 6 periods of 6 years each. To obtain equal periods, years 1969 and 1970 were excluded. For each period, species regularity was calculated as the number of years in which the species were recorded at least once (range 0-6). In addition, we estimated an index of relative abundance for each period and species on a scale from 0 to 3, in which 0 was defined as not observed, 1 as observed in low numbers, 2 as observed in moderate numbers, and 3 as observed in high numbers. Thresholds for each category were defined within each period by a visual inspection of the distribution of the number of records per species. Numerically, the threshold between low and moderate corresponded approximately to the 50% percentile of species, while between moderate and high to the ~90% percentile. This method aims to correct for among-year differences in observational effort, which may result in different numbers of observations as it re-scales the total number of observations for a species according to the total number of observations per period. Therefore, index values among periods are perfectly comparable. Thresholds used are shown in Table 1. Finally, based on frequency and relative abundance quantified for each species, we classified them in a category of the wintering status as follows:

- 1 (erratic): Present in half of the years at maximum (< 3) with low abundance (0-1).
- 2 (irregular): Present in most years (4-5) but in low to moderate abundance (1-2).
- 3 (regular): Present in most years (4-5) with moderate to high abundance (2-3). Also those species occurring all the years (6), but in low abundance (1)
- 4 (established): Present in all years (6) in moderate to high numbers (2-3).

The list of score assigned to each species for regularity, abundance and the resulting wintering status for each period is given in Supplementary Table S1.

2.4 Ecological and phenological data of the study species

We collected 21 variables with the aim to identify phenotypic and ecological characteristics of the species that may favour establishment of a wintering population north of the Sahara desert (see the complete description in Table 2). Whenever possible, variables were considered only for western European populations, because these populations are expected to be those from which wintering populations in Iberia and Morocco originate. Variables showed a notable degree of collinearity (mean absolute r = 0.257, s.d. = 0.225). For this reason we performed a Principal Component Analysis (PCA) in order to reduce dimensionality. This analysis was conducted using 69 species for which we had complete information for the 21 variables (values shown in Supplementary Table S2). The number of principal components was visually determined by the change in the slope of the plot of eigenvalues. Selection was further supported by the eigenvalues of the components, and the cumulative percentage of variance explained. Components were varimax rotated to enhance their interpretation. Principal component analysis yielded 5 major components (Table 3) that explained 80.23% of the total variance and that we subsequently used as predictors in the Generalized Estimating Equations (GEE) (see 2.5 and 2.6). The first principal component (PC1) grouped mainly variables related to the spring phenology of the species. Larger values of PC1 implied species with later spring migration and onset of breeding, and consequently with a shorter stay in the European breeding areas. PC2 was closely related to the traditional winter distribution of the species in Africa. Positive values of PC2 represent species with the large wintering areas, i.e. with more southern wintering latitudes and large migration distance. PC3 was predominantly related to the variables describing the timing of autumn migration. Large values of PC3 are related to late autumn migratory and to a long periods stay in Europe. PC4 represents among-species variation in breeding latitudes. Large values were found in species with breeding areas in central and northern Europe. The last component (PC5) represents variation related to the end of the breeding season. High values of this component are related to a late end of the reproductive season. This component is also positively related, but to a smaller extent, to variation in body mass.

Period	Total no. of records	Mean no. of records per species	Low (1)	Moderate (2)	High (3)
1971-76	137	1.63	01-feb	03-abr	> 5
1977-82	262	3.11	01-feb	03-abr	> 5
1983-88	544	6.47	01-mar	abr-13	> 13
1989-94	2254	26.83	01-jun	jul-70	> 70
1995-00	3169	37.73	ene-28	29-103	> 103
2001-06	2970	35.36	ene-25	27-89	> 90

Table1
Criteria used for the classification of abundances of species in each time period (see 2.3 for details)
.

	Variable name	Description
1	**European Population** [log(nºpairs)]	Number of pairs of western Europe
2	**Northermost breeding latitude** (Lat º)	Northern limit of breeding range (Max 70ºN)
3	**Southermost breeding latitude** (Lat º)	Southern limit of breeding range in Europe (Min 36ºN)
4	**Breeding range extension** (Lat º)	Difference in latitudinal degrees between northern and southern limit of breeding range
5	**Mean breeding latitude** (Lat º)	Mean value between northern and southern edge of the breeding range
6	**Northermost wintering latitude** (Lat º)	Northern limit of the traditional sub-Saharan wintering range (Max 26ºN)
7	**Southermost wintering latitude** (Lat º)	Southern limit of the traditional sub-Saharan wintering range (Min -12ºS)
8	**Wintering range extension** (Lat º)	Difference in latitudinal degrees between northern and southern limit of traditional wintering range
9	**Mean wintering latitude** (Lat º)	Mean value between northern and southern edge of the traditional wintering range
10	**Migration distance** (Lat º)	Difference in latitudinal degrees between the mean breeding and the mean wintering latitude
11	**Start of the breeding season** (weeks)	Week number in which mating activities begin
12	**End of the breeding season** (weeks)	Week number in which chicks fledge from the nest
13	**Mean of the breeding season** (week)	Mean week between the start and the end of the breeding activities
14	**Start of spring migration** (weeks)	Week number in which departures from wintering grounds begin
15	**End of spring migration** (weeks)	Week number in which arrivals to the breeding gorunds conclude
16	**Mean of spring migration** (weeks)	Mean week between the departures of the wintering grounds and the arrival at the breeding quarters
17	**Start of fall migration** (weeks)	Week number in which departures from breeding grounds begin
18	**End of fall migration** (weeks)	Week number in which arrivals to the wintering ground conclude
19	**Mean of fall migration** (weeks)	Mean week between the departures from the breeding grounds and the arrival at the wintering quarters
20	**Length of the period spent north of the Sahara** (weeks)	Number of weeks elapsed between mean spring and mean fall migration
21	**Body mass** [log(g)]	Mean adult body mass of the species, sex pooled

Table 2

List and description of the 21 ecological and phenological variables collected for 69 species of trans-Saharan European birds. Information was obtained from Cramp (1977-94), with the exception of the spring migration phenology of Erythropygia galactotes that was found in SEO/Birdlife (2013). Phenological variables are given in calendar week, numbered from 1 to 48 (year considered composed by 12 months of 4 weeks each as in Cramp 1977-94*).*

	PCA 1	PCA 2	PCA 3	PCA 4	PCA 5
Eigenvalue	5.37	4.26	3.45	2.29	1.48
% of explained variance	25.57	20.30	16.44	10.89	7.03
European Population [log(nºpairs)]	0.081	-0.275	0.088	0.577	-0.578
Northermost breeding latitude (Lat º)	0.009	0.271	-0.145	**0.900**	0.067
Southermost breeding latitude (Lat º)	0.038	0.176	-0.624	0.410	0.121
Breeding range extension (Lat º)	-0.016	0.183	0.264	**0.729**	-0.008
Mean breeding latitude (Lat º)	0.023	0.271	-0.376	**0.823**	0.100
Northermost wintering latitude (Lat º)	-0.454	-0.184	-0.241	-0.168	-0.274
Southermost wintering latitude (Lat º)	-0.080	**-0.960**	-0.089	-0.137	-0.083
Wintering range extension (Lat º)	-0.114	**0.891**	-0.014	0.067	-0.034
Mean wintering latitude (Lat º)	-0.233	**-0.882**	-0.163	-0.177	-0.170
Migration distance (Lat º)	0.189	**0.800**	-0.046	0.511	0.176
Start of the breeding season (weeks)	**0.725**	0.106	0.164	-0.021	0.386
End of the breeding season (weeks)	-0.055	0.015	0.251	0.140	**0.851**
Mean of the breeding season (weeks)	0.312	0.063	0.271	0.096	**0.834**
Start of spring migration (weeks)	**0.843**	0.089	-0.178	-0.159	-0.013
End of spring migration (weeks)	**0.856**	-0.051	0.045	0.197	-0.089
Mean of spring migration (weeks)	**0.970**	0.030	-0.089	0.000	-0.054
Start of fall migration (weeks)	0.147	0.033	**0.802**	-0.250	0.153
End of fall migration (weeks)	-0.073	0.173	**0.708**	0.345	0.243
Mean of fall migration (weeks)	0.045	0.123	**0.904**	0.055	0.237
Length of the period spent north of the Sahara (weeks)	-0.605	0.072	0.735	0.041	0.213
Body mass [log(g)]	-0.219	0.429	0.072	-0.454	0.547

Table 3.
Results from the Principal Component Analysis conducted with 21 ecological and phenological variables of 69 species of European trans-Saharan migrants. In bold, factor loadings > 0.7 in absolute value.

2.5 Analysis of ecological and phenological factors determining the wintering probability

We estimated the effect of the ecological variables on establishment probability by fitting Generalized Estimating Equation (GEE) models, accounting for the phylogenetic relatedness among species.

Species cannot be considered as independent samples because they share a common evolutionary history, which leads closely related species to share the same or quite similar traits (Felsenstein 1985). Therefore, phylogenetic relations between species have to be taken into account, to avoid statistical pseudo-replication. We did this by constructing a phylogenetic tree for the previously selected 69 bird species. We obtained 3,500 trees from the web birdtree.org (Jetz et al. 2012), using the "Hackett All Species" tree source. We than computed a consensus tree with MEGA 5.1 (Tamura et al. 2011), considering solved branches with bootstrap values higher than 70. The resulting tree

presented no polytomies. We then rechecked the structure of the tree, comparing it with published phylogenies in order to check for eventual incoherencies. With this approach, we finally moved the relative positions of *Hirundo rustica, Delichon urbicum* and *Hirundo daurica*, following Sheldon et al. (2005). The final resulting tree is shown in Figure 1.

We tested for the effects of the previously obtained principal components (see 2.5) representing among-species ecological and phenological variation (shown in Table 3) on the probability of establishment of wintering populations north of the Sahara. To this aim we built a binomial response variable, defined as species with established (wintering status 3 and 4) *vs* species with non-established populations (wintering status 1 and 2) in the Western Mediterranean during the period 2001-2006 (see Figure 4 below). In addition to the 5 principal components resuming eco-phenological traits, in the models, we also included as predictors population trends reported by EBCC (2004) for the periods 1970-1990 and 1990-2000. We performed generalized estimating equation (GEE) models using the ape v.6 package in R (Paradise et al. 2004). We tested all models both with Martins's (Martin and Hansen 1997) and Brownian (Felsenstein 1995) phylogenetic correlation structures (see ape manual and references therein for details: http://cran.r-project.org/web/packages/ape/ape.pdf.

We did not test the models with the other available correlation structures because we had no reasons to assume a non-constant rate of evolutionary change (as in Blomberg's structure) or a non-equal branch length in the considered phylogeny (as in Grafen's structure). The models with Martins' correlation structure, which we finally chose, showed lower QIC (equivalent to AIC for GEE models, see Pan 2001) values than the ones obtained applying a Brownian model (details not shown for brevity). We ran all the 127 possible models given by the combination of the 7 predictors, as well as the null model with a constant as predictor. For all models, we calculated the correspondent QIC values. The 128 models were thereafter ranked by increasing QIC values (see in Table 4 the top 30 models). In addition, as further test of the robustness of the obtained model, we also selected the best model by progressive backward exclusion of non-significant factors, starting from the full model, which included the 7 predictors.

2.6 Reliability and potential biases of the data

In spite of the fact that any wintering record of a trans-Saharan bird north of the Sahara is of great interest for ornithologists, the main problem of this type of data is that it is not collected following standardized protocols. Therefore, the distribution of records may be biased by spatial or temporal variations in observer effort (Kujala et al. 2013). Moreover, species differ in their detectability and consequently, more detectable species becoming those with more chances to be recorded during the winter. To test for the reliability of our data, we carried out a couple of control tests:

2.6.1 Comparison between standardized censuses and literature surveys

During the period 2007-2010, standardized censuses of the bird populations occurring in Spain during the winter were carried out as part of the field sampling for the Atlas of Birds Wintering in Spain (SEO/Birdlife 2012). Such censuses provided a standardized quantification of wintering bird populations, including the trans-Saharan species found during these censuses. The same atlas also gathered data of rare wintering species observed outside of the standardized sampling transects during 2007-2010. This is the case of occasional observations of rare wintering species directly communicate to the authors of the atlas or published in other journal and later compiled by the authors of the atlas. Thus, for 64 species considered in our study, the Spanish Atlas provide two different values of winter abundance, one gathered by standardized census and a second obtained by non-standardized observations and bibliography research. This second method is similar to the one that we used for building our database. We found a significant and positive correlation between log-transformed abundances obtained by standardized and non-standardized techniques for the 64 species of trans-Saharan birds reported in the atlas (Pearson's r = 0.594; p < 0.001). Therefore, non-systematic recorded data published in literature provide a reliable estimation of wintering populations of trans-Saharan birds because the species wintering in larger numbers are those more frequently cited.

2.6.2 Comparison between wintering status categories

The Atlas of Birds Wintering in Spain (SEO/Birdlife 2012) divided the species that were observed during the census in three groups: modelled (enough data to develop a predictive model on winter presence), only sporadic cites, and without data. These categories can be considered three categories of decreasing abundance and are roughly similar to our categorization of the wintering status described in section 2.3, but it was carried out independently of us by the authors of the bird atlas for all the 80 species that we studied. Given that the Atlas is based on data collected in 2007-2010, just after the end of the time window that we considered, we predicted that if our classification of species status for the period 2001-2006 was accurate, there should be a good correspondence with that classification for atlas data for the period 2007-2010. For instance, to be modeled in the atlas, a species should be established during the winter. However, if a species has been not detected during the atlas execution, its wintering occurrence should be erratic. We compared both classification systems by a non-parametric correlation and found a significant correspondence between the two classification systems (Spearman's rank correlation p= 0.496; p << 0.001). We can thus conclude that standardized methods and casual records compiled from literature provide a similar picture of the status of trans- Saharan birds in winter.

Figure 1
Phylogenetic tree for the 69 species considered in GEE models.

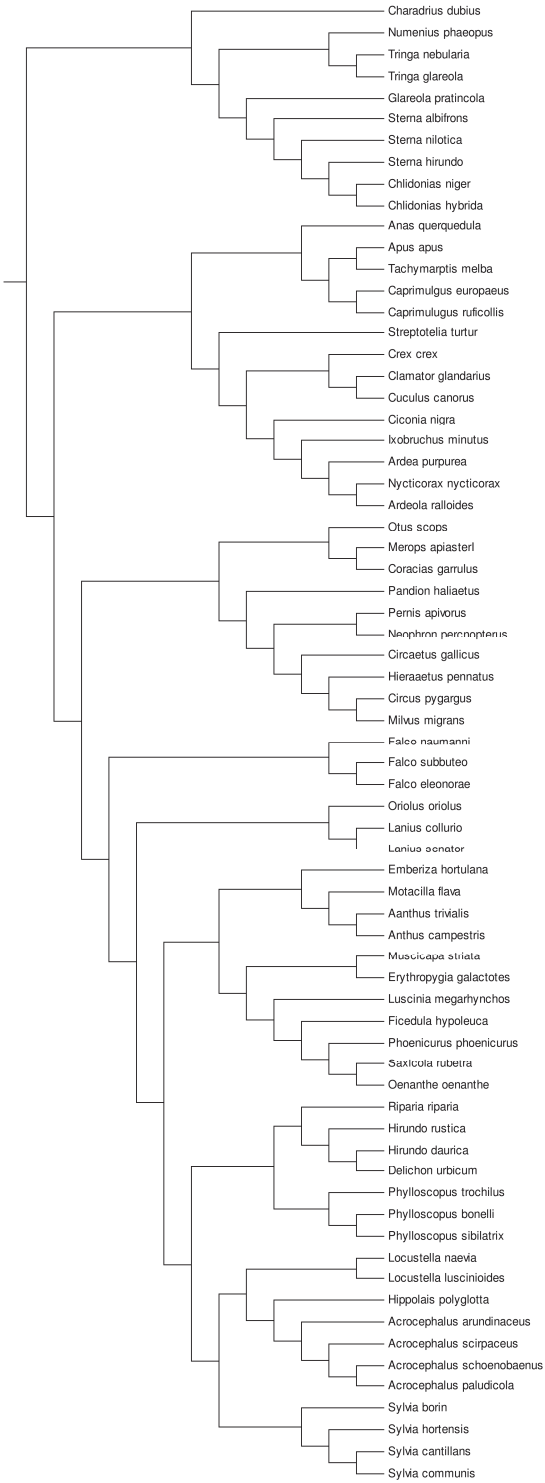


Table 4

Best 30 GEE models predicting the establishment of wintering populations north of the Sahara. For selection of models we used the information criterion QIC, which is equivalent to AIC for likelihood based models (Pan 2001). PC1 to PC5: Principal components given in Table 3. Pop7090: European population trend between 1970 and 1990. Pop9000: European Population trend between 1990 and 2000 (EBCC 2004).

Ord.	Model	QIC
1	PC1 + PC2 + PC5	63.503
2	PC1 + PC2 + PC5 + POP7090	64.234
3	PC1 + PC2 + PC4 + PC5	65.038
4	PC1 + PC2 + PC5 + POP9000	65.182
5	PC1 + PC2 + PC3 + PC5	65.344
6	PC1 + PC2 + PC3 + PC5 + POP7090	65.816
7	PC1 + PC2 + PC4 + PC5 + POP7090	66.119
8	PC1 + PC2 + PC5 + POP7090 + POP9000	66.147
9	PC1 + PC2 + PC4 + PC5 + POP9000	66.739
10	PC1 + PC2 + PC3 + PC4 + PC5	66.775
11	PC1 + PC2 + PC3 + PC5 + POP9000	67.003
12	PC1 + PC2 + PC3 + PC4 + PC5 + POP7090	67.661
13	PC1 + PC2 + PC3 + PC5 + POP7090 + POP9000	67.717
14	PC1 + PC2 + PC4 + PC5 + POP7090 + POP9000	68.033
15	PC1 + PC2 + PC3 + PC4 + PC5 + POP9000	68.432
16	PC1 + PC2 + PC3 + PC4 + PC5 + POP7090 + POP9000	69.560
17	PC1 + PC2	73.630
18	PC1 + PC2 + POP7090	75.439
19	PC1 + PC2 + PC3	75.452
20	PC1 + PC2 + PC4	75.527
21	PC1 + PC2 + POP9000	75.647
22	PC1 + PC5	76.573
23	PC1 + PC2 + PC3 + POP7090	77.225
24	PC1 + PC2 + PC3 + PC4	77.303
25	PC1 + PC2 + POP7090 + POP9000	77.406
26	PC1 + PC2 + PC4 + POP7090	77.407
27	PC1 + PC2 + PC3 + POP9000	77.471
28	PC1 + PC2 + PC4 + POP9000	77.539
29	PC1 + PC5 + POP9000	77.826
30	PC1 + PC5 + POP7090	77.835

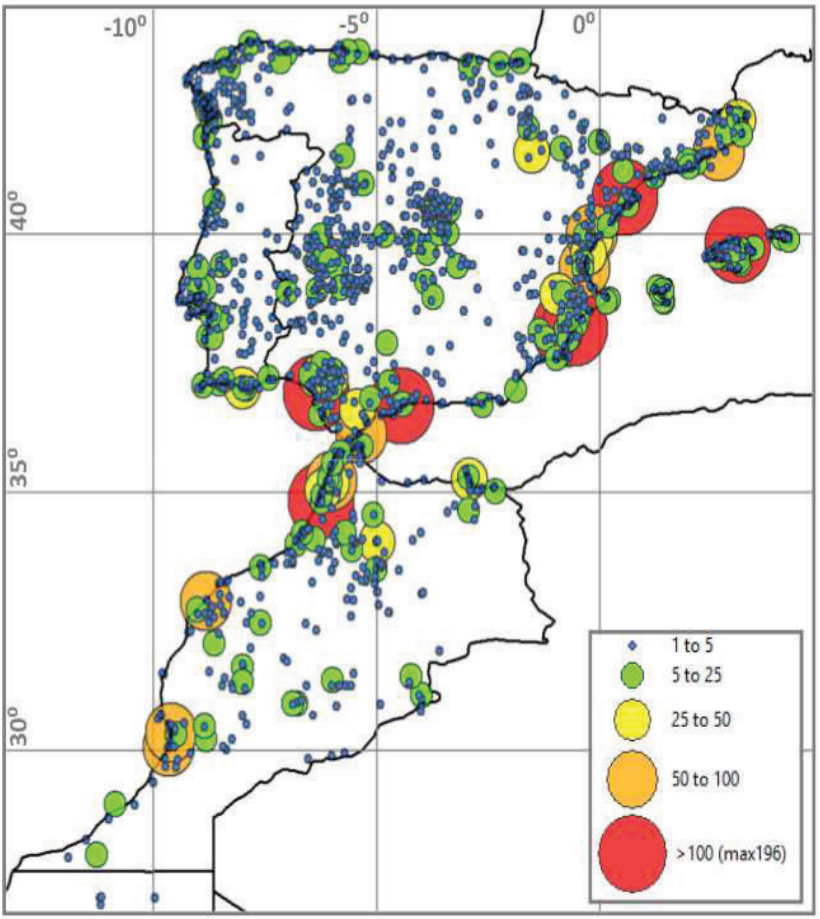


Figure 2
Geographical distribution of the winter observations of the 80 studied species of trans-Saharan migratory birds along the southern edge of the European Western flyway between 1969 and 2006.

3. Results

3.1 Species abundance and trends of wintering north of the Sahara

Our analysis of wintering observations demonstrated that wintering north of the Sahara is a common phenomenon in trans-Saharan migrants. Yet, the number of reported wintering events was unevenly distributed among species, ranging from 1 in the wood warbler, *Phylloscopus sibilatrix* to 539 in the booted eagle, *Aquila pennata* (see Supplementary Table S1). Trans-Saharan migrants were predominantly found in coastal wetlands, particularly in Northern Morocco, southern and western Spain (Figure 2), possibly representing those areas with the mildest winter climate.

The number of wintering records of trans-Saharan species significantly increased over time (GLS result: coefficient = 0.038, SE = 0.013, p = 0.0061). We observed the strongest increase between 1985 and 1994 (Figure 3a). Analysing passerine and non-passerine species separately, it becomes apparent that changes in wintering behaviour have been larger in non-passerines than in passerines (Figure 3a; coefficient for non-passerines 0.044, SE = 0.011, p < 0.0001; coefficient for passerines: 0.034, SE = 0.008, p < 0.0001). Similar results were obtained when we analysed temporal variation in the number of individuals per reported observation (Figure 3b). In 43 of the 80 species studied, group sizes significantly increased over time (GLS: p<<0.001,Figure 4). This was due to the increase in numbers in non-passerines (GLS: p=0.004). In passerines, we found no significant overall increase in mean group size (GLS: p=0.213). This effect may partly be due to the fact that most passerine species are not gregarious, and some are territorial in winter. Models run at the specific levels lead to similar results, whereby coefficients of the effect of year were mainly positives (Figure 4). These series of models had significant results only in those species with positive slopes, indicating an increase in the number of wintering events (Figures 4a and 4c) or in the number of individuals per observations (Figures 4b and 4d).

Analyses based on the qualitative wintering index (see 2.4) indicate that the number of species that have established wintering populations north of the Sahara has strongly increased in the past 35 years. While at the beginning of the study (1969-1976) only 18 % of the species were regularly observed north of the Sahara in winter (status 3-4), two dec ades (1989-1994) 50% of the species had established winter populations (Figure 5). Thereafter, the ratio of established versus non-established species remained constant (Figure 5). By the end of the study (2001-2006), the proportion of species that had established wintering populations in the Mediterranean was significantly higher in non-passerine than in passerine species (Fisher's Exact Test on two categories: *p = 0.00011; Risk Ratio = 2.67*).

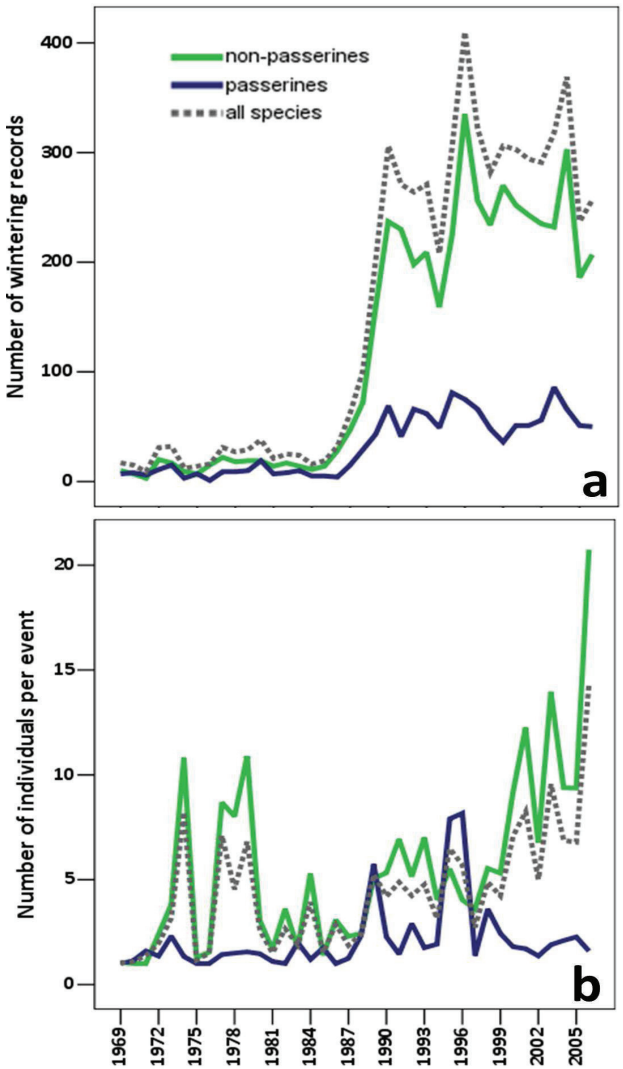


Figure 3
(a) Number of wintering observations reported for 80 trans-Saharan migrants in Spain, Portugal and Morocco between 1969 and 2006 (dotted line). The numbers for passerine species (n=1235, blue line) and non-passerine species (n=4551; green line) are shown separately. (b) Number of individuals per observation.

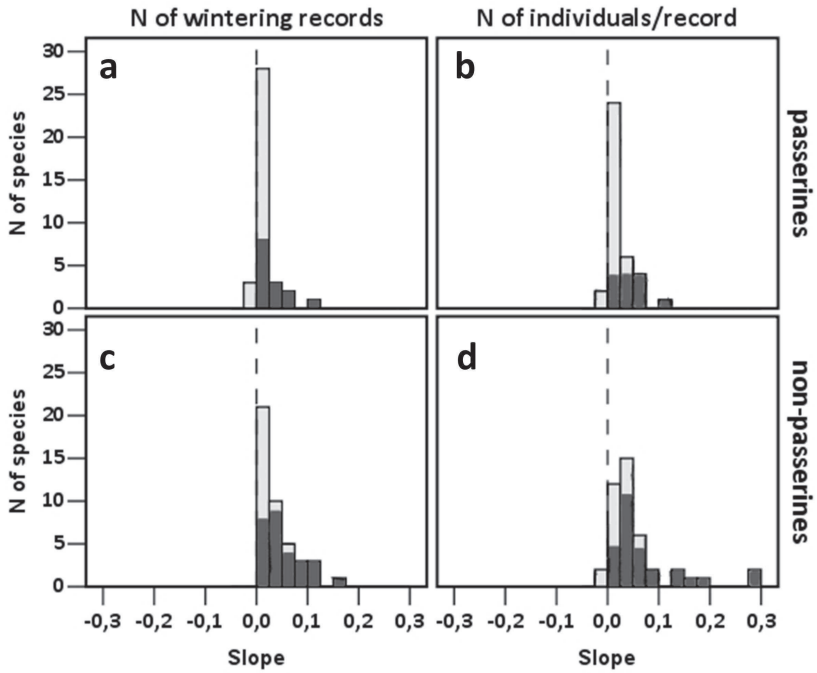


Figure 4

Distribution of the slopes of the species-specific GLS exploring the temporal trend of number of wintering records north of the Sahara (a,c) and number of individuals for each record (b,d) in 37 passerines and 43 non-passerines species of European long-distance migrants. Positive values of the slope indicate an increase in the considered value between 1969 and 2006. Black bars represent models significant at the 0.05 level.

3.2 Factors facilitating the probability of establishing wintering populations north of the Sahara

The best model obtained through backward exclusion of non-significant variables corresponds with the best one obtained by the QIC criteria. This final model and the relative coefficients are shown in the box in Figure 6. The effects of species-specific ecological and phenological features (expressed by the PCs) on the probability of establishing wintering populations north of the Sahara (see 2.6) resulted to be higher than population trends in the same time windows, given that both trends referring to 1970-1990 and to 1990-2000 were excluded from the models (Table 4). In particular, GEE models revealed that the first principal component (PC1), was the most important variable, being present in 100% of the best models (Table 4). Almost equally important was the effect of PC2, which was included in 90% of the best models (Table 4). Thus,

species that migrate and start breeding early in spring (PC1) and have large wintering ranges (PC2), and as a consequence long migration distance, are more likely to establish wintering populations north of the Sahara (quadrant I in Figure 6). Species migrating and breeding late in spring and wintering with small wintering ranges tend not to become established (quadrant III in Figure 6).

Figure 5

Change of wintering status of 80 European trans-Saharan migrants in the western Mediterranean region between 1971 and 2006. Wintering status was determined considering abundance and regularity of a species in winter within each of the six 6-year periods. Shading give different wintering status categories (black = fully established, dark grey = almost established, light grey = irregular, white = erratic). The dotted red line gives the proportion of established species (wintering status 3 and 4).

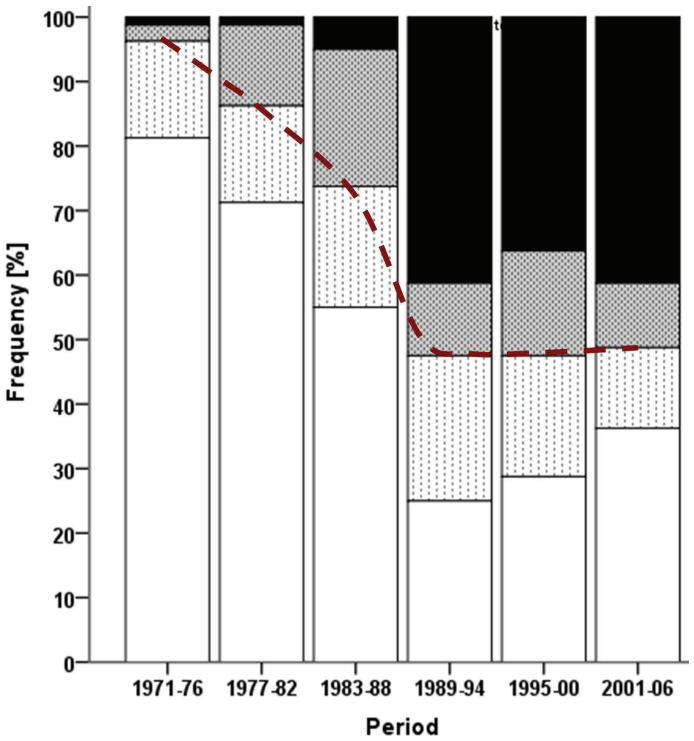
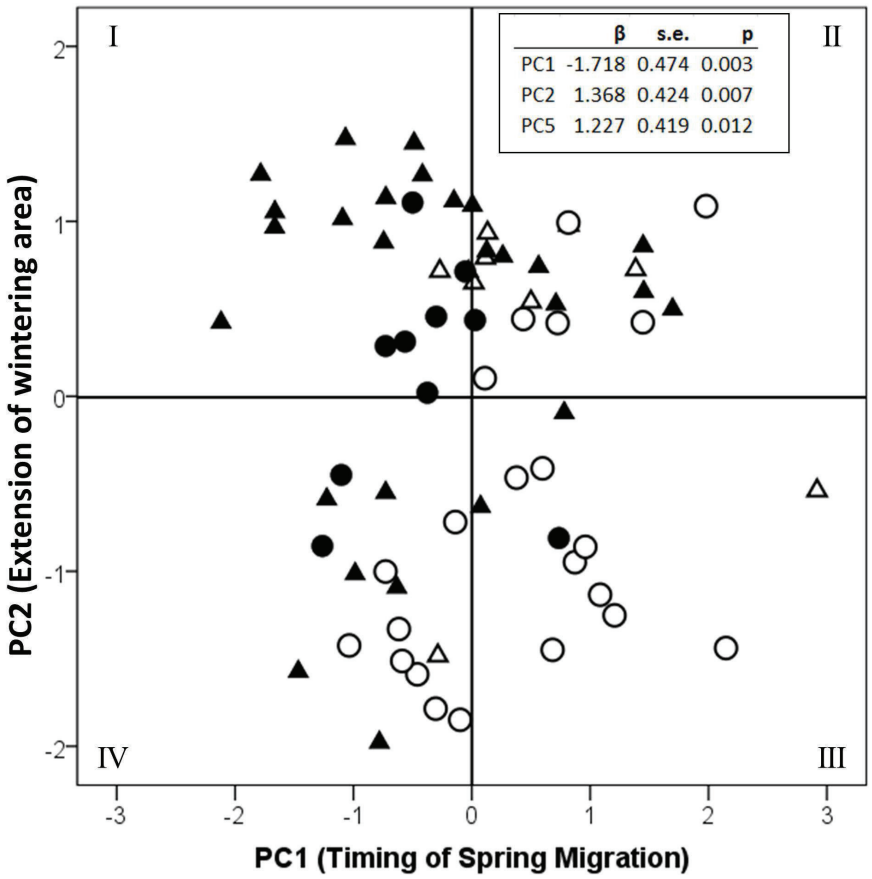


Figure 6

Distribution along two axes of "ecological variables" of 69 species of trans-Saharan migrants (passerines = dots, non-passerines = triangles), which have been successful (filled symbols) or unsuccessful (open symbols) in establishing wintering populations north of the Sahara at the end of the study period (2001-2006). PC1 represents variation in the timing of spring events. PC2 represents variation in the size and location of the "traditional" wintering range and of migration distances (see table 3). Birds with early spring migration (negative PC1) and a large wintering range (positive PC2) have been more prone to establish wintering populations in the Mediterranean Region. Box in quadrant II show the coefficients of the best GEE models of the factors affecting probability of establishing wintering populations north of the Sahara.



4. Discussion

Our study demonstrates that many long-distance migrants have the potential for rapidly shifting the northern edge of their wintering ranges to the north. In the past 35 years, many trans-Saharan migrants have established small populations wintering in the Mediterranean Basin that have been rapidly growing. However, there are marked differences among different groups of long-distance migrants. In accord with previous studies (see chapter 21 in Newton 2008), we found that changes in migration are more frequent and more pronounced in non-passerine than in passerine species. These differences in adaptability are likely to be due to differences in the control of migration. Birds with a social control of migration, as found in many non-passerines (e.g. storks, cranes, ducks, geese), may rapidly modify migratory habits due to high phenotypic plasticity (Hötker 2002, Mueller et al. 2013). In contrast, migration in passerines, particularly, in long-distance migrants, is primarily controlled by an inherited migration programme (Berthold 1996 and 2001), with little phenotypic plasticity, which results in a reduction of phenotypic variation (Pulido and Widmer 2005, Pulido 2011). We therefore expect the establishment of new wintering quarters in passerines to require evolutionary changes, as observed in central European Blackcaps that started to winter in UK (Berthold et al. 1992). However, it is unlikely the displacement of wintering areas across the Sahara observed in this study, resulted from an evolutionary process, since this would have required the gradual shortening of migration distance (Pulido et al. 1996, Coppack et al. 2008), which would have implied successfully wintering in the Saharan Desert, a hostile area of at least 1500 km width. The fact that in our study only 30% of passerine species succeeded in establishing wintering populations north of the Sahara is in line with this idea. Interestingly, all swallow species investigated made this range shift. These species are characterized by migrating during daytime and in groups, in contrast to most other passerine species. The establishment of new wintering areas in these species, like in most non-passerines, is likely to have result from learnt and socially transmitted changes in migration habits (Hötker 2002, Mueller et al. 2013), which may also have involved evolutionary changes in physiological response to the environment (Coppack and Both 2002). Apart from the differences in adaptive capacity that that we found between passerines and non-passerines, we found that the ecological characteristics of the species influenced the probability of shortening migration distance. Species migrating and breeding early in spring and with large wintering ranges and long migration distances are more likely to establish wintering populations north of the Sahara.

One possible explanation for this pattern may be that the advantage of shortening migration distance is larger for those species that arrive earliest in spring, which are those that supposedly experience strongest selection for earl arrival. However, considering the short

time in which changes have taken place, it is more likely that differences in the probability of establishing new wintering areas are due to differences in ecological tolerance ranges rather than to differences in selection intensity. Early-migrating species are more exposed and, therefore, are expected to be more tolerant, to conditions of food shortage and inclement weather. Species with a large wintering range and, as a consequence, large migration distances, have more plasticity in the physiological response to alterations in the photoperiod, which is a physiological prerequisite for adaptive changes in wintering latitudes (Coppack and Pulido 2004). So, which consequences have these findings for the adaptation and survival of long-distance migratory birds facing global change? If, as predicted, the northward shift of wintering ranges is an adaptation to climate change, we would expect that these shifts have had a measurable effect on the rate of adaptation of species. It has been hypothesized that the shortening of migration distance facilitates an advancement of migration and breeding in spring (Berthold 2001, Coppack and Both 2002, Visser et al. 2009), which is the clearest adaptive response of migratory birds to recent climate alterations (Knudsen et al. 2011). The direct impact of this shift in wintering range should be related to species-specific changes in the timing of spring migration for northwestern European populations. This would allow testing whether wintering closer to the breeding grounds is one of the mechanisms underlying the recent advance in migration and breeding observed in many populations of trans-Saharan migrants (Coppack and Pulido 2004, Pulido 2007b, Visser et al. 2009, Ambrosini et al. 2011).

Yet, irrespective of whether there is a causal link between the shortening of the migratory distances and the advancement of spring phenology, the capacity for establishing wintering areas to the north to the current wintering range could be used as an indicator of the adaptive potential of a migratory species facing current climate change. Species that have shifted their wintering range to the north are likely to be those species with the highest potential for phenotypic adjustment to environmental changes, and therefore the least vulnerable. One of the major challenges for the future will be identifying the driving factors of this process, which may be complex, due to carry-over effects between different stages of the annual cycle (Harrison et al. 2011). We predict that those populations of long-distance migrants that are currently wintering north of the Sahara will further grow, and will colonize new areas to the north of their current winter distribution. We expect those species that failed to establish new wintering populations in the 35 years of this study to suffer population declines in the future, unless they can adapt to changing environmental conditions by other mechanisms, yet to be identified. Monitoring population changes during reproduction and winter will help us to elucidate the dynamics and importance of this process. This will help us to identify and preserve new wintering areas of pivotal importance for the adaptation of long-distance migrants to climate change (Lehikoinen et al. 2013).

5. Supplementary Tables

Printed versions of these tables are available in supplementary materials at the end of the volume. To access electronic version, click or copy and paste the following links in your browser.

Table S1
List of the 80 species of European trans-Saharan migrant birds for which wintering record at north of the Sahara were collected. For each 6-year period the values of regularity (Reg.) and abundance (Ab.) and the consequent qualitative wintering status (scoring 1-4) are given (see Methods for an explanation of the scoring). Total numbers of wintering records for each species over the whole period are also given.
https://dl.dropboxusercontent.com/u/22345958/SuppMat%20MM%20thesis/Chapter%20II/table%20s1%20chapter%20II.pdf

Table S2
Specific values of the 21 variables listed in Table 2 for each of the 69 species considered.
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CHAPTER III

Shortening of migration distances in birds is not explained by recent climate warming

Michelangelo Morganti, Oscar Gordo and Francisco Pulido.
Unpublished manuscript.

Abstract

Climate change is causing profound changes in the behaviour of migrating species. Drawing on the recent reduction of migration distance observed in Palaearctic short-distance migrants, and on the detection of selective pressures favouring earlier arrival at the breeding grounds, it has been predicted that trans-Saharan migratory birds should start wintering north of the Sahara as a response to climate warming. Here, we empirically tested the relationship between temperature changes and the shortening of migration distance in European trans-Saharan birds during last decades. To this aim we analysed all published wintering records of 77 trans-Saharan migrants in the Iberian Peninsula and Morocco between 1969 and 2006. We run species-specific generalized least squares models to directly compare if the numbers of birds wintering north of the Sahara were related to temperature changes at the species-specific breeding sites, in the areas of autumn passage or in the potential wintering sites at north of the Sahara.
Number of individuals wintering at north of the Sahara significantly increased in 42 (55 %) of the studied species. However, in most species this increase was not associated with temperatures experienced during any considered stage of the life-cycle. Yet we found a tendency for wintering numbers to increase when winter temperatures experienced the previous year were higher. We also found a weak negative effect of temperatures experienced during autumn migration on the probability of wintering north of the Sahara. Our results suggest that temperature change per se is not the main driver of recent alterations in the migratory behaviour of long-distance migrants. The deterioration of environmental conditions in the traditional sub-Saharan wintering quarters and the spread of human-related food resources that are available year-around in Iberia and Morocco may have favoured shortening of migratory distance more than climate warming.

1. Introduction

Climate change is affecting a wide range of biological features of organisms (Parmesan 2006, Letcher 2009). Migratory species are expected to be among the most affected species because they have complex life cycles in which successive phases are spent in different geographical areas (Robinson et al. 2009). Birds have been object of a wide range of studies and have become a model for the study of climate change impacts on migration (Møller et al. 2004 and 2010, Knudsen et al. 2011, Pautasso 2012). Current climatic changes impose new selective regimes and may represent a serious threat for the conservation of migratory birds (Berthold et al. 1998, Both et al. 2006, Møller et al. 2008, Saino et al. 2011).

At regional scale, poleward shifting of geographical ranges and distributional limits is expected (Parmesan et al. 1999, Hickling et al. 2006, Møller et al. 2010), while at a local scale, advancement of plant and insect spring phenology (Menzel et al. 2006, Thackeray et al. 2010) causes strong selection favouring earlier arrival dates of birds (e.g. Both et al. 2006, Jónzen et al. 2007). At a continental scale, these two effects will ultimately promote a common adaptive response in migratory birds: the reduction of migration distances (Coppack and Both 2002, Fiedler 2003, Visser et al. 2009). Winter distribution of many bird species at temperate latitudes have actually moved northwards in the last decades (Valiela and Bowen 2003, Austin and Rehfisch 2005, La Sorte and Thompson 2007, MacLean et al. 2008, Lehikoinen et al. 2013). In parallel, some intra-palearctic migrants have shown a shortening of their migratory distances (van Vliet et al. 2009, Visser et al. 2009, Smallegange et al. 2010, Heath et al. 2012) and even microevolutionary changes leading towards reduced migratory activity have been found (Pulido and Berthold 2010). All these phenomena concur with predicted range shifts under a warming scenario. However, only few studies have empirically tested the relationship between climate and changes in migratory distances or spatial distribution (Jukema and Hulscher 1988, Austin and Rehfisch 2005, Ambrosini et al. 2011, Heath et al 2012, Sanz-Aguilar et al. 2012).

Currently, predictions of the effect of climate change on migratory distances are supported by empirical results obtained for short to medium-distance migrants, but there is little information on how long-distance migrants respond to the same selective pressures (e.g. Martínez & Sánchez-Zapata 1999, Fiedler 2001). Generally, a shortening of migration distance for this group of species is also expected (Berthold 2002, Fiedler 2003, Coppack and Pulido 2004, Pulido 2007b). Indeed, the observed advancement of dates of migration to breeding areas observed in many trans-Saharan species (Cotton 2003, Lehikoinen et al. 2004), indicates that strong selection in the breeding areas is favouring this phenotypic change. However, adaptive changes may also be determined by selective factors in the wintering areas (Gordo et al. 2005,

Gordo and Sanz, 2008, Zwarts et al. 2009). Moreover, shortening of migration distance for long-distance migrants may be constrained by several evolutionary and ecological factors. It is well-established that in many species migration is controlled by inflexible endogenous programs, which impose timing and direction of migration (Berthold 1996, Newton 2008), and is often associated with reduced phenotypic variance, thus limiting the adaptive potential for these species (Pulido and Widmer 2005). In addition, ecological barriers, as the Sahara desert that separate European breeding and African tropical wintering areas, may prevent any progressive approach due to its ecological unsuitability (Pulido et al. 1996, Coppack et al. 2003, Gordo 2007, Coppack et al. 2008).

Many trans-Saharan bird species have started wintering at north of the Sahara in the last decades (Chapters I and II), suggesting that they have shortened their migration distance along the Western-European flyway. In the present study, we profit of the same database used in the previous chapters to test for the role of temperatures at different times of the year and in different areas in driving the establishment of the new wintering quarters north to the Sahara in European long-distance migrants. We propose three non-exclusive hypotheses (Figure 1):

a. Winter-conditions amelioration hypothesis (H1 and H1b)

Harsh and limiting environmental conditions during winter in temperate and boreal regions have been postulated as one of the main selective factors shaping migratory behaviour in those populations breeding there (Newton 2008). If winter climate in these areas becomes milder due to global warming, one predicts that bird survival during that season will increase (Lemoine and Böhning-Gaese 2003). In the particular case of trans-Saharan bird species, this fact would mean that individuals wintering north of the Sahara (e.g. in the Mediterranean basin) would have a higher probability of survival and, as a consequence, that this new migratory behaviour will spread in the population. The effects of winter temperatures on the abundance of birds wintering at temperate latitudes could be mediated by two different mechanisms: one would be a plastic response to milder temperatures (H1), i.e. the warmer the winter the larger the proportion of wintering long-distance migrants. mediated by selection. The hypothesis H1b is dependent on 1) a higher reproductive success of birds with shorter migration and 2) significant heritability of the migratory traits. The first condition is expected because by moving the wintering area northwards individuals may save time and energy in migration and consequently, their early arrival may enhance their synchronization with ecological conditions in breeding areas (Coppack and Both 2002, Fiedler 2003, Pulido 2007a). The second condition has been demonstrated to be met in many wild populations, even if it probably occurs through genetic transmission of migratory program among short lived small-sized birds (Pulido and Berthold 2003, 2010) while

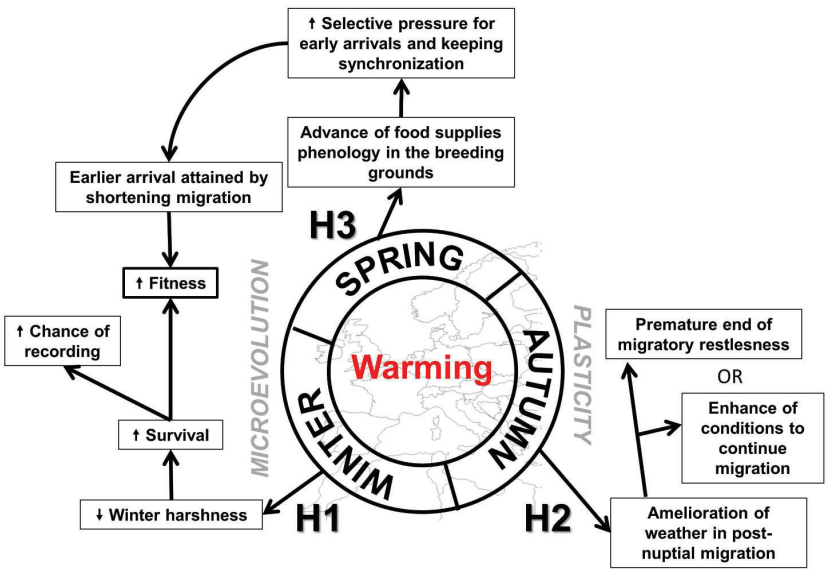
is probably achieved by cultural transmission of migration pattern in big-sized long lived birds (Mueller et al. 2013).

b. Autumn decision hypothesis (H2)

Weather conditions experienced en route affect migration progression and stopover decisions (Gordo 2007, Tøttrup et al. 2008, Mellone et al. 2012). Therefore, environmental conditions during the post-nuptial migration may favour a premature end of the migration (H2). For instance, in the white stork (*Ciconia ciconia*), it has been demonstrated that eastern European populations may stop their migration in the Sahel depending on the amount of rainfalls there in the preceding months and thus, on the food availability

Figure 1

Conceptual framework of the hypothesis tested in this manuscript. Climate warming in Western Europe had different consequences on long-distance migratory birds depending on the phases of life cycle in which occur. Climate warming in winter may ameliorate conditions for wintering, thus directly enhancing probability of wintering at north of the Sahara (H1). This effect may be better expressed in terms of survival of the individuals showing the new behaviour and thus may eventually emerge with a 1-year lag (H1b, see Introduction). Growing of temperature experienced during autumn migration may promote the suspension of migration at these latitudes but is also possible that have the opposite outcome, given that high temperatures promote prosecution of migration (H2). Warming of spring temperatures cause strong selective pressure favouring an advancement of arrivals to the breeding grounds, which may be attained by shortening the migration distance (H3). Responses to the mechanisms tested in H1 and H3 are more associated to genetic (microevolutionary) changes, while the one tested in H2 is more due to plasticity of migratory behaviour (phenotypic plasticity).



prospects for the winter (Zwarts et al. 2009). This process would rely on the plasticity of the migratory behaviour and thus, it is expected in species with a flexible control of migration, i.e. with environmentally and socially mediated migratory behaviour (Sutherland 1998, Newton 2008, Mueller et al. 2013). Climate seems a suitable cue for individual birds taking the decision to overwinter at more northern latitudes. However, two alternative predictions can be formulated: (1) If temperatures in late summer-autumn are a reliable predictor of winter temperatures, one would expect more individuals shortening their migration in years in which they experience high temperatures in the areas of passage during autumn migration. (2) If high temperatures in late summer-autumn negatively affect productivity during winter (e.g. Horion et al. 2013), one would expect a negative relation between autumn temperatures and the number of long-distance migrants spending their winter in mid-latitudes.

c. Spring advancement hypothesis (H3)

Synchronization with food sources during reproduction is a major ecological factor imposing strong selection on the timing of spring migration (Visser and Both 2005, Møller et al. 2010, Visser 2012). Therefore, the date of arrival at the breeding grounds must be finely tuned for being able to take advantage of the peak of food availability in spring. Consequently, we expect intense selection on this phenological trait (Møller et al. 2008, Saino et al. 2010). By shortening the migratory journey, long-distance migrants may achieve an earlier arrival to the breeding grounds, thus keep pace with the phenological advance of spring during the reproductive season (Coppack and Both 2002, Pulido 2007b, Coppack et al. 2008). Moreover, being exposed to northern photoperiods in winter induces earlier gonadal development and migration (Coppack et al. 2003, 2008, Coppack and Pulido 2004). Therefore, one may predict a positive correlation between spring temperatures in the areas of reproduction (i.e., a proxy for the advancement of spring) and the abundance of migratory birds wintering in mid-latitudes. This may result from a microevolutionary process by which individuals that winter in areas located closer to the areas of reproduction would have a selective advantage by being better synchronized with environmental conditions during reproduction. Alternatively, and in a non-excluding way, this change in wintering latitude may be a consequence of behavioral plasticity based on learning. Birds could phenologically adjust their reproductive cycle in response to conditions experienced in the previous year (Grieco et al. 2002). Bird experiencing a warm spring and consequently mistimed reproduction will remain at northern latitudes in the following winter, in order to compensate for the delay in arrival and “re-synchronize” with the phenology in the breeding areas (i.e. peak of availability of caterpillars for chicks’ raising).

In this study we tested these three, non-exclusive hypotheses for 77 species of European long-distance migrants,

occurring along the western European flyway. We tested in species-specific models the influence of temperature changes in the respective breeding quarters, in areas of passage during autumn migration and in the new wintering areas north of the Sahara (Western Mediterranean). We aim to disentangle the role of climate to provide a mechanistic evolutionary-based response for the recently observed shifts in the migratory distance of trans-Saharan birds.

2. Methods

2.1 Wintering birds' data

We gathered all published citations of trans-Saharan bird species observed in Spain, Portugal and Morocco during winter. These observations are of special relevance due to their rarity and for this reason they are regularly published in local and regional ornithological journals and reports of those countries. The bibliographic search yielded 363 publications containing pertinent information (see Annex 1 for the complete list of references). Due to the inter-specific differences in migration phenology, we defined a species-specific wintering period according to the migration dates across the Strait of Gibraltar (see Supplementary Table S1). Only those citations of a species within its wintering temporal window were considered. We excluded all records in which the observer suggested a possible very late or very early migrant, and all the cases in which the bird was found dead. A total of 5,752 winter records were gathered concerning 77 species between 1969 and 2006. We defined a "wintering event" as any observation irrespective of the number of individuals reported. For further details on the data recompilation see Chapters I and II.

2.2 Meteorological data

Data were obtained from the NCEP/NCAR Reanalysis project (Kanamitsu et al. 2002) by using the RNCEP 1.05 package for R software (Kemp et al. 2012) as daily mean temperatures for cells of 2.5º longitude x 2.5º latitude covering Western Europe and Morocco (latitude range: 27ºN to 70ºN; longitude range: -10ºW to 20ºE; see Figure 2) between 1969 and 2006. Temperatures were temporally and spatially averaged for species-specific time periods and areas, depending on the phenology and breeding distribution of each species (shown in Figure 2 and Table S2). Thus, we built explanatory variables fitted to each species for each one of our study hypotheses (see Introduction).

2.3 Bird phenology and breeding distribution

In order to test the hypotheses 2 and 3, we obtained for each species the passage dates across Iberia in autumn and the arrival dates to the European breeding areas from the phenological diagrams provided by Cramp (1977-94).

We defined a short time frame (one week) and a long time frame (five weeks) for each species in both migratory periods. In the short time frame, we assumed the last week of fall migration across Europe as the moment in which the species mainly cross Iberia and the last week of spring migration as the moment in which the species mainly arrive at their breeding quarters. Instead, the long time frame corresponds to the central week within each migratory period (spring or autumn) with a buffer of two weeks before and after (see Table S1 for the list of the phenological periods). The long time frame reduces the stochastic variability introduced in the temperature data series when considering a one week period. The average breeding latitude of each species was calculated by distribution maps in Cramp (1977-94) considering only western European populations. We considered only Western Europe because we had only wintering data for Iberia and Morocco, which are considered the passage areas of the western European populations of trans-Saharan migrants. The breeding distribution was used to obtain an accurate geographical range for temperature time-series used to test the spring driving hypothesis (H3). The average breeding latitude in Western Europe was rounded to the nearest latitude with available temperature data, so i.e. a species which mean breeding latitude was 41º had been included in the "40º group". Longitudinally, these latitudinal bands were limited to the cells mainly covering land (see Figure 2 for breeding areas defined according to groups of cells).

2.4 Statistical analyses

Temporal trends of temperatures were calculated for the period 1969-2006 for the specific month-area combinations by means of simple regressions against year. Thus, we analyzed temperatures for winter months in Iberian and Moroccan cells (H1), autumn temperatures in the Iberian Peninsula (H2) and spring temperature trends in Europe (H3).

Climate effects on wintering events of trans-Saharan birds were tested by General Least Squares (GLS) models of the nlme package of R software (Pinheiro et al. 2012). The number of wintering events of each species (our response variable) was square-root transformed prior to analyses to achieve normality. Explanatory variables were constituted by the four temperature time-series corresponding to our hypotheses (see introduction). These variables were obtained by calculating average values with the appropriate time lag and spatial area for each species. For winter months (H1), we used mean temperature values of cells covering Iberia and Morocco within each species-specific winter period. We also included this variable with a lag of one year to test for potential carry-over effects of the survival in a winter on the probability of overwintering north of the Sahara in the following year (H1b). To test H2, we included the mean values for cells covering only Iberia and for the species-specific autumn migration temporal window. Finally, the fourth included

climate predictor in the models aimed to test H3. It was a species-specific temperature series at the mean breeding latitude at the time of spring arrival. The models were repeated twice, one with the short- and another with the long time frame described for H2 and H3. Year was included as predictor in all the models to control for the potential confounding effect of a temporal collinearity between temperatures and the number of wintering events. In addition, we accounted for the potential temporal auto-correlation of observational data by including an autoregressive term of order 1 (Zuur et al. 2009). We used a model of order 1 because more complex structures (e.g. second, third, etc. order autoregressive terms) were not statistically significant.

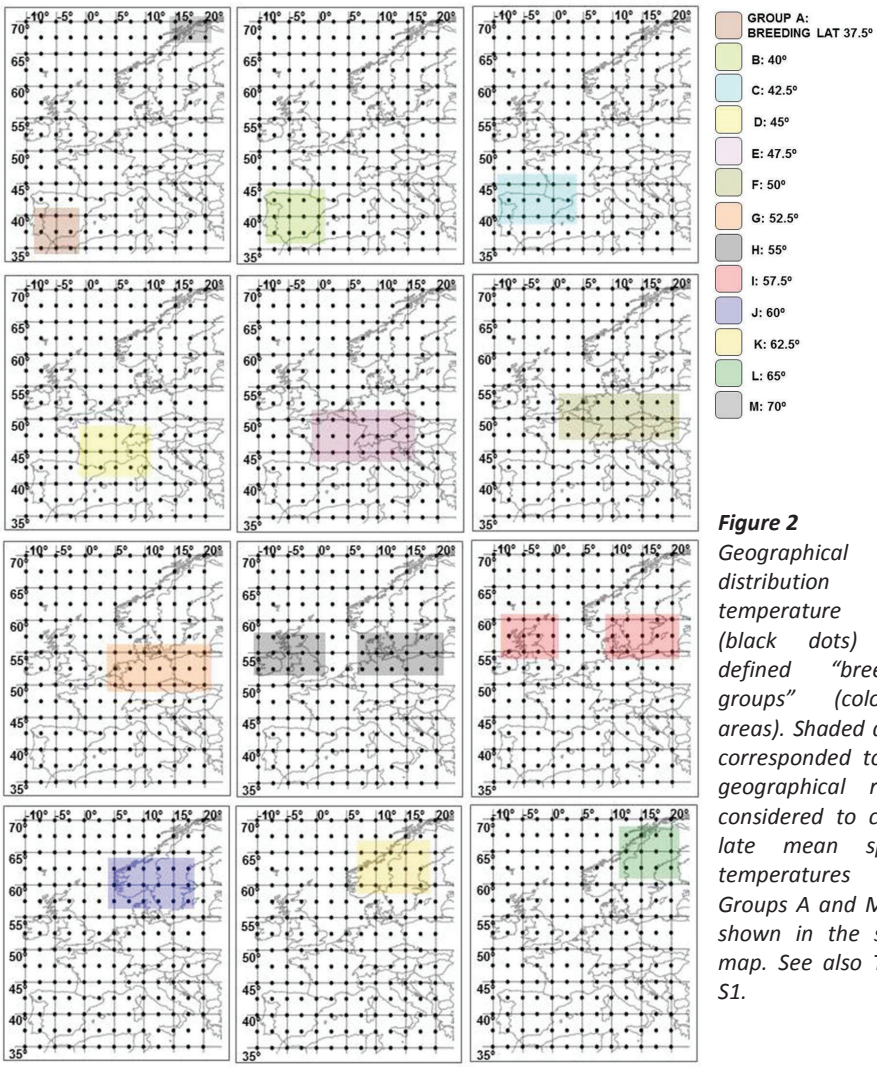
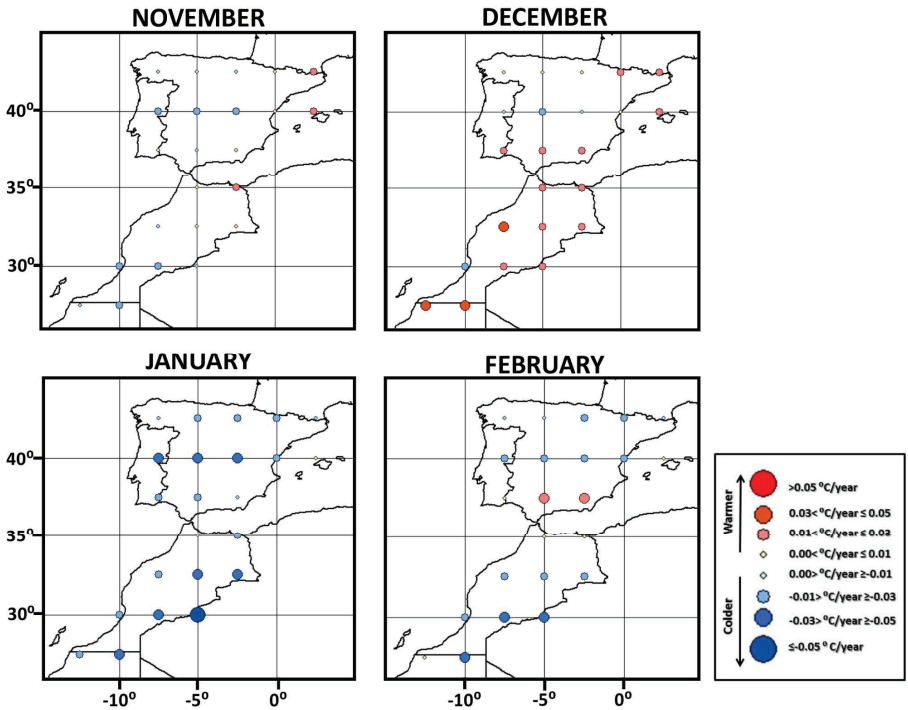


Figure 2
Geographical distribution of temperature data (black dots) and defined "breeding groups" (coloured areas). Shaded areas corresponded to the geographical range considered to calculate mean spring temperatures (H3). Groups A and M are shown in the same map. See also Table S1.

Each model was run twice, with and without the autoregressive term and likelihood ratio tests were carried out to determine the significance of this random term (Zuur et al. 2009). The autoregressive term was included in the models, if it was statistically significant at $p<0.05$. Finally, for each species, we carried out a null model (with no explanatory variables in) and through likelihood ratio tests we estimated the overall significance of the previous models.

Figure 3

Temperature trends in the Western Mediterranean between 1969 and 2006 for the "wintering" months (November to February). See colour scale for correspondence.



3. Results

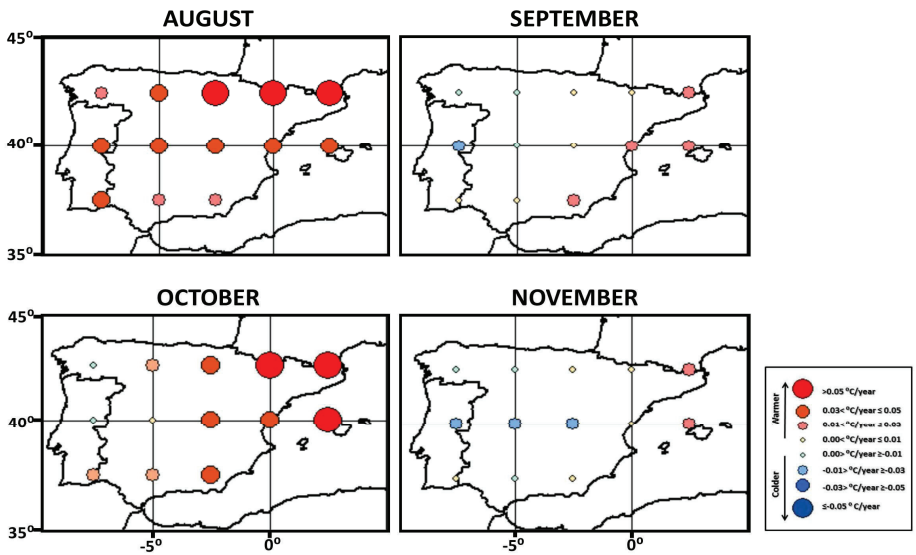
3.1 Temperature trends

Mean winter (November to February) temperatures in Iberia and Morocco showed in most cases slight tendencies to colder temperatures during the study period (Figure 3). However, they were statistically significant only in four cells for the month of January (27.5N/10W,

30N/7.5W, 30N/5W, 40N/5W). Temperatures in the autumn migration period in Iberia showed some warming, especially in eastern Iberia in August and October (Figure 4). Mean temperatures during spring months increased between 1969 and 2006 over most parts of Europe, but some heterogeneity among regions in the magnitude and even sign of the temporal shift is found (Figure 5). In March, May and June, warming was especially intense from 50º southwards, while in April warming was strongest around the 55º of latitude. Interestingly, temperature over Scandinavia became colder in June and partially in May. In sum, temperature trends showed marked heterogeneity among seasons and regions, suggesting that climate change may have produced different selective pressures on migratory traits expressed during each moment of the year.

Figure 4

Temperature trends in Iberia between 1969 and 2006 for the "autumn migration" months (August to October). See colour scale for correspondence.

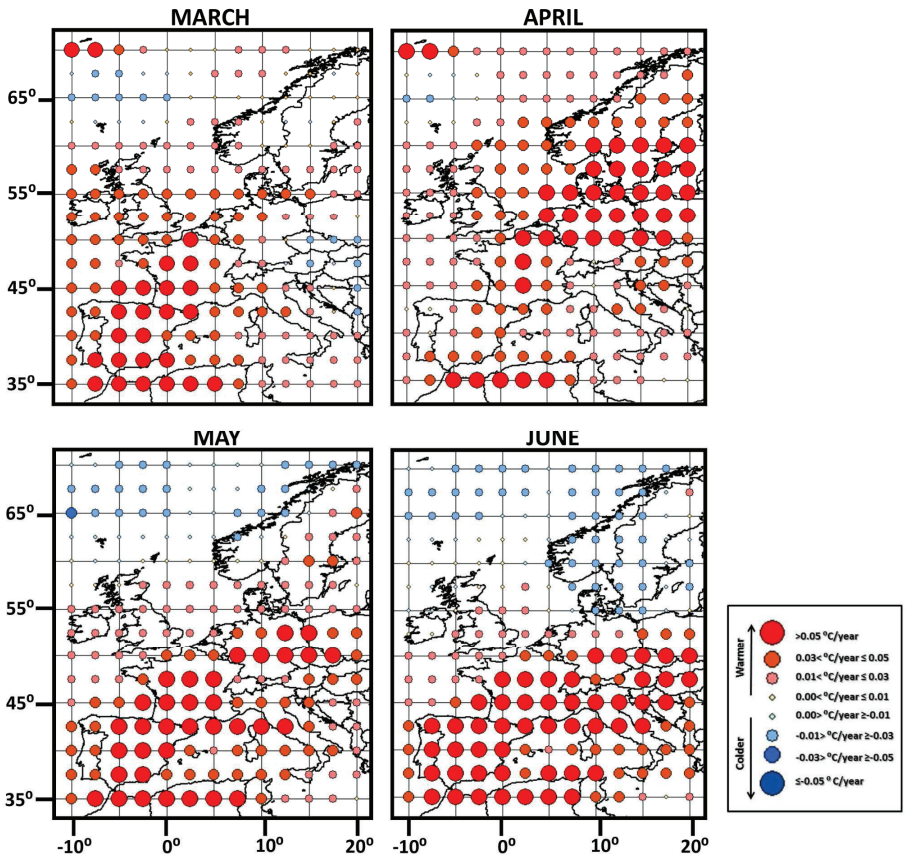


3.2 Climate effects on wintering events in Western-Mediterranean

Overall, there were no strong effects of temperature variables on the number of wintering events of trans-Saharan birds observed in the Western Mediterranean between 1969 and 2006. Although a few species yielded some statistically significant effects of temperatures, in most cases they showed no coherent patterns in favour of any of our hypotheses (Figure 6). Year was by far the variable with the largest effect. It was significant in 40

Figure 5

Temperature trends in Europe between 1969 and 2006 for the "spring migration" months (March to June). See colour scale for correspondence.



and 42 out of 77 species in both types of models (i.e., 1-week or 5-week temporal frame of temperature variables). In all the species in which was significant, year has a positive effect meaning that overall there was an increase in the occurrence of trans-Saharan birds during winter in the Western Mediterranean since 1969 (Figure 6). Models in which we used a 5-week time window for spring and autumn temperatures ("Models 2" in Table S2B) had generally lower AIC values than those models that included variables of 1-week time window (models 1; compare Table S2A and S2B). This fact suggests that weather over longer periods is better fitted to decisions on whether to cross the Sahara or not (Table S2). In 43 species, we found a statistically significant model (the same number for both types

of models), although year was the only significant explanatory variable in most cases. In 23 species, no model was significantly fitted to data, suggesting that in these species the number of wintering events did not change over time and

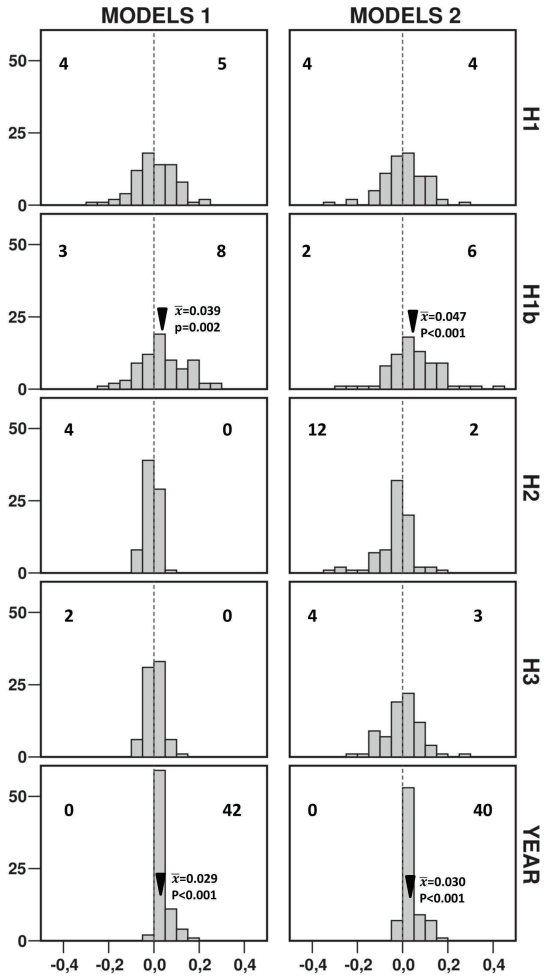


Figure 6

Distributions of the model parameters of the explanatory variables in the models of type 1 and 2. Models of type 1 used a temporal window of 1 week for the explanatory variables, while models of type 2 a window of 5 weeks (see Methods for details). Positive parameters mean that the number of trans-Saharan birds wintering in the western Mediterranean is larger under warmer temperatures. Black triangle marks the average parameter when significantly different from 0. The number of species with significant effects is indicated in the corners of graphs (right: positive, left: negative). H1: winter temperatures, H1b: winter temperatures of the previous year, H2: autumn temperatures, H3: spring temperatures.

among-year variations were not related to climate fluctuations. In 6 species, the models obtained using the short time frame of 1-week were not significant, while models reached significance when autumn and spring temperatures were calculated using the larger time-frame of 5-weeks. This suggests that one or both factors are actually related to the number of wintering events for that species.

Overall, H1 (winter temperatures of the same year) and H3 (spring temperatures) had the smallest support among all the explanatory variables. The average slope for H1 and H3 for the 77 studied species was not significantly different from 0 in both cases irrespective of the time frame used for the exploratory variables (Figure 6). The number of slopes with positive and negative signs was equally distributed, strongly suggesting that the observed pattern is merely stochastic. For a significance threshold of α=0.05, one would expect 4 cases out of 77 to be significant by chance. In fact, we found 9 cases for H1 and 2 cases for H3.

Winter temperatures of the years preceding the observation (H1b) had an overall positive effect, which significantly differed from 0 (Figure 6). Almost in every species in which was significant, the slope was also positive. This suggests that warm winter temperatures enhance bird survival north of the Sahara and such response can be detected in the following year.

The distribution of autumn temperature (H2) slopes suggests that higher temperatures in this time of the year have a negative effect on the probability of wintering north of the Sahara (Figure 6). This is suggested by the accentuated negative skewness of this distribution in both models and by the fact that in almost every cases in which H2 results are significant, the sign of the slope is negative.

4. Discussion

Most of the 77 studied trans-Saharan bird species increased their numbers of effectives wintering north of the Sahara between 1969 and 2006, suggesting a shortening of their migratory distances. However, this behavioural change was overall not strongly related neither to the amelioration of winter climate in the western Mediterranean nor to the selective pressures induced by the advancement of spring in the breeding areas, nor to weather-related decisions during the autumn migration. Thus, our fine-scaled approach, in which we accounted for specific differences in phenology and distribution, suggests that recent changes in temperature do not seem to be the direct cause of the recent shortening of migration distance in western European long-distance migrants. However, the marked heterogeneity in the biology of the studied species may prevent the detection of a general and common response.

4.1 Winter amelioration hypothesis

Winter harshness is the most important factor determining mortality among wintering birds (Newton 1998, 2008). Thus, anyone expects a northward shift of wintering ranges of birds in parallel to the progress of global warming (Matthews et al. 2004, Huntley et al. 2007). This expectation has been indeed demonstrated by empirical data in several taxonomic groups (Parmesan et al. 1999, Hickling et al. 2006, La Sorte and Thompson 2007, Visser et al. 2009, Heath et al. 2012). However, in our study, the necessary condition for this hypothesis does not hold because winter temperatures have not changed during the last decades in the Western Mediterreanean (Figure 3).

Therefore, if winters are not warmer, wintering populations of trans- Saharan birds cannot increase in response to more favourable climate-related survival.

Nevertheless, the number of wintering events in a year seems partially determined by temperatures experienced in the previous winter, thus giving some support to our hypothesis H1b. Even for those species that did not increase their occurrence in winter, inter-annual variation in the number of wintering events was somehow dependent on the temperature of the previous winter.

These evidences fit well with a scenario in which wintering latitude is a-priori genetically determined and its success is given by the simple survival of the individuals showing the "anomalous" behaviour. At the same time, this shows that the ultimate cause generating a spread of the northern-wintering behaviour must be others than changes in winter temperatures, being these only a factor that potentially contain the success of the new behaviour by reduced survival of the fraction of individuals that winters north of the Sahara compared to the ones that follow on with the typical long-distance migration. Individuals of the same population that overwinter at different latitudes (non-breeding partial migration, Chapman et al. 2011) can show different survival rates, and this is demonstrated to be a mechanism that can maintains the variability of migrating behaviour in a certain population, being the survival probability of the ones that undertake the longest migration almost stable year-by-year while the one of the short-distance migrants can oscillate from much higher to much lower than the other fraction of the population depending on the harshness of the winter (e.g. Sanz-Aguilár et al. 2010, Lok et al. 2011). Extreme cold winters in particular can dramatically reduce the number of short-distance migrants in the population, ultimately avoid that this behaviour became unique among the population (Sanz-Aguilár et al. 2010, Lok et al. 2011). Of course, temperatures experienced during winter not only have immediate consequences as survive or not survive but affect fitness in the following reproductive seasons via carry-over effects (Harrison et al. 2010) and this must be taken into account to correctly evaluate costs and benefits of strategies.

4.2 Autumn decision hypothesis

Higher temperatures in Iberia during fall migration result to be associated to a lower number of birds staying north of the Sahara in winter for many species. This result would support that warm weather in late summer-autumn may be related to lower productivity and thus resources during the winter (see Introduction). Actually, warm autumns are associated to low values of the Normalized Difference Vegetation Index (NDVI, a proxy of vegetation productivity) in Mediterranean areas (Horion et al. 2013). Autumn is a key season in Mediterranean ecosystems due to its peak of rainfalls. Warm temperatures in autumn could be related to drier conditions, which reduces vegetation productivity and as consequence have a negative impact on food availability both in autumn and later in winter. Additionally, temperature favours departure decision from stopover sites as well as migration rate during fall migration, both in passerines (Morganti et al. 2011) and non-passerines (Mellone et al. 2012). Under these conditions, the enlargement of migration would be promoted, reducing the proportion of birds that stop migration at Mediterranean latitudes and overwinter there.

4.3 Spring advancement hypothesis (*pulling* hypothesis)

Spring advancement is considered the most important factor affecting the observed shifts in bird migration patterns at temperate latitudes (Knudsen et al. 2011). However, we did not find any effect of temperature experienced during this season on the probability of remain and overwinter in the Western Mediterranean. Thus, the hypothesis that a shortening of migratory distance may have been selected via an increased reproductive success of those individuals remaining in the Mediterranean basin by an improved phenological matching with their resources during reproduction is not supported. In our study, we did not find evidence that this adaptive mechanism is operating in the same way among different species at a wide geographical scale but we cannot exclude that this is occurring in particular populations. For instance, selection for earlier arrivals at the breeding quarter is thought to have driven the observed northward shift in the African wintering quarter of the Barn swallow (*Hirundo rustica*) (Ambrosini et al. 2011). Different rates of warming in spring temperatures in each part of the breeding range (Ahola et al. 2004, Both et al. 2004, Both and te Marvelde 2007) or even in each time of the spring (Doi et al. 2008) may prevent a common general response.

4.4 Environmental changes in the traditional wintering areas as possible driving selective factor (*pushing* hypothesis)

Climate has changed in the traditional sub-Saharan wintering quarters of the studied species during the last decades (Hulme et al. 2001, Nicholson 2001) and this may have had some effect on the migratory behaviour of birds (Ambrosini et al. 2011). It is well established that population dynamics of trans-Saharan birds are affected by winter ecological

condition in the Sahel (Szép 1995, Newton 2004, Gordo 2007), a wintering core area for many of the populations studied here. Ecological conditions in the Sahel were harsh until the 90s due to persistent droughts that have caused a vast reduction in the seasonal flooded areas (Zwarts et al. 2009) and primary productivity (Anyamba et al. 2005). Aridity conditions establishing the ecological southern border of the Sahara desert are subject to strong yearly latitudinal oscillations (Tucker and Nicholson 1999), possibly causing that the band in whch these oscillations occurs do not accomplish the ecological needs of species in search of the conditions found in the traditional semiarid wintering quarters of the Sahel. Ultimately, trans-Saharan migrants need to migrate longer to reach the "Sahelian conditions" they need. In parallel, increased temperatures in temperate and boreal latitudes has shifted northwards the breeding ranges (Huntley et al. 2007, Møller et al. 2010, Chen et al. 2011). Thus, an extension of the migratory distances is expected (Barbet-Massin et al. 2009, Doswald et al. 2009). This fact directly increases time and energy costs of migration and adds to the increased mortality suffered by many populations in the Sahel during the last decades (Zwarts et al. 2009). As a result, the balance between costs and benefits of the long- (sub-saharan Africa) vs. the short-distance migration (Mediterranean) seems clearly disrupted, favouring those individuals staying at new wintering areas north of the Sahara. The role of wintering habitat quality as selective pressure acting on the adaptive shortening of migration distance by "pushing" the wintering birds northward seems the key to understand in part the observed increase in the recurrence of wintering events in the Western Mediterranean. Zwarts and colleagues (2009) suggested that such a process already took place among some species that shifted the center of gravity of their wintering areas northward some decades ago, eventually "unhooking" the dependence of their population dynamics from the negative trend in ecological conditions in the Sahel. Population trends for these species (e.g. White stork, Spoonbill *Platealea leucorodia*, Marsh harrier *Circus aeruginosus* and Little egret *Egretta garzetta*), are the few to be positive among European long-distance migrants, suggesting that establishing new wintering quarters at European latitudes would be enormously beneficial for populations. However, populations of other species, such as the Barn swallow, currently lie in a larger proportion in drier and warmer areas near of the southern boundary of the Sahara, which may have contributed to the general decline of the species (Ambrosini et al. 2011). Moreover, some other species actually still find good conditions in their traditional wintering quarters, such as the whinchat *Saxicola rubetra* (Hulme and Cresswel 2012). Therefore, there is a marked idiosyncrasy in the species-specific susceptibility to ecological conditions in the sub-Saharan areas, which is largely due to differences in habitat preferences and/or trophic niches (Zwarts et al. 2009). These

species-specific differences would prevent the emergence of a common response to the changes occurred in sub-Saharan traditional wintering quarters, that only for some species would effectively be the shortening of migratory distances and the wintering at north of the Sahara.

4.5 Alternative hypotheses to climate: human induced changes in the new Mediterranean wintering areas

Some anthropogenic processes have notably altered important ecological conditions for birds during the winter in the Western Mediterranean. One of the most important is the appearance of a new, predictable, and virtually unlimited food source all year-round as outdoors refuse dumps (Donazár 1992). For example, the amount of organic refuse in Spain constantly increased till 2003; here, about 13 millions of tons of refuses are annually stored in dumps accessible for birds (data from the Spanish Ministry of Agriculture, Food, and Environment www.magrama.gob.es). Dumps are actually used by wintering birds (Senar and Borrás 2004) and had been very likely a concurrent factor in favouring wintering at this latitude for some species, especially raptors, herons, storks, and gulls (Negro et al. 1991, Gómez Tejedor and de Lope 1993, Blanco 1996, Garrido and García-Sarasa 1998, Gómez-Tejedor 1998, Marchamalo et al. 1998, Camiña and Montelío 2005). The number of winter citations in the Western Mediterranean of Black Kites *Milvus migrans* increased three orders of magnitude but none of the temperature variables studied was related to it (see Table S2). However, it is one of the most common raptors in dumps due to its scavenger feeding (Garrido and García Sarasa 1998, Camiña and Montelío 2005, De Giacomo and Guerrieri 2008). Another paradigmatic case is the white stork *Ciconia ciconia*. We did not include this species in our study because it regularly overwinters in Iberia since the 1980s (Máñez et al. 1994, Marchamalo et al. 1998, Molina and Del Moral 2005) and no winter citations have been published since then. It has been suggested that sedentariness of this species has been promoted by the use of refuse dumps and the spread of some invasive species, such as crayfishes (Máñez et al. 1994, Gordo and Sanz 2006, Zwarts et al. 2009). Moreover, individuals exploiting refuse dumps raised about 40% more chicks than those feeding in natural areas (Tortosa et al. 2002), promoting a strong natural selection of this behavior. Interestingly, raptors, herons and storks were some of the species with the most pronounced change in their migratory behaviour (see Table S2) as well as in their population numbers (Molina and Del Moral 2005, Palomino 2006, Garrido et al. 2012, Palomino et al. 2013) suggesting that this spreading of outdoors refuse dumps may be functioning like a large scale experiment of supplementary feeding. In fact, supplementary feeding by human activities had been shown to facilitate survival and reproduction success in many species of birds, sometimes even promoting range expansions (Robb et al. 2008). The observation that urban Blackbirds *Turdus merula* tend to be more resident then their rural

conspecifics in the northern edge of its distribution suggests that supplementary food promote residency via enhanced probability of winter survival (Evans et al. 2012). Dependence on anthropogenic provisioning of food to support wintering populations can be so strong that Avilova and Eremkin (2001) suggested that number of Mallards (*Anas platyrynchos*) wintering around Moscow have decreased because people stopped to feed as a consequence of the economic crisis in Soviet Union after 1989. Long-lived bird species, such as raptors, herons or storks, show a strong plasticity in their migratory behaviour (Berthold et al. 2002, Alerstam et al. 2006, Trierweiler et al. 2012) and thus, an adaptive behavior, such as using new feeding opportunities offered by refuse dumps, could spread in the population really fast. Finally, changes in land-use, as the spreading of olive-groves, on which some passerine species can feed in winter (Senar and Borrás 2004), or other extensive cultures, could have improved wintering conditions for other trans-Saharan species in Mediterranean latitude. As example, the lengthening of the wintering stay in Iberia of the frugivorous short-distance migrant *Turdus philomelos*, is suggested to have been induced by changes in management of the olives fields (Gordo and Sanz 2005), so that this could be a resource making viable the wintering at this latitude, at least for the species that are able to feed on fruit during winter. The spread of rice-fields that remains flooded during winter had expanded the availability of wetland surface, favouring the spread of directly associated species as herons and waders (Fasola and Ruiz 1996). Given that wetlands are the main habitat where trans-Saharan migrants occurred in winter in Spain (Morganti and Pulido 2012, Chapter I), and the same pattern is maintained also for the observations occurred in Portugal and Morocco (Chapter II), the spread of artificial wetlands could have favoured also the presence in winter of bird species that do not directly feed on flooded surface. Furthermore, many wetlands area have been progressively included in wide conservation programs as the UNESCO Ramsar Convention from 1975, and reduction of human-induced mortality in these areas could have been a concurrent factor in making it more suitable for wintering birds (Fasola et al. 2010).

4.6 Adaptive constrains for bird migration

About one third (23) of the species did not show any temporal change in the number of wintering citations. These were mainly passerines species, a group for which the inability to undertake adaptive changes in migration patterns had been repeatedly suggested (Sutherland 1998, Pulido and Widmer 2005). Populations of these species show little phenotypic plasticity on migration-related traits because of their strong environmental canalization (e.g. *Sylvia borin* Pulido and Widmer 2005). Moreover, many populations of trans-Saharan migrants are indeed declining (BirdLife International 2004, Pearce-Higgins et al. 2009, Vickery et al. 2014) being such decline especially notable in long-distance migrants overwintering in

the Sahel (Zwarts et al. 2009). Smaller populations may be constrained in their adaptive responses because of their reduced genetic variability (Gordo and Doi 2012a and 2012b), limiting even more options for phenotypic variability in these species with a strong, inflexible and endogenous control of migration. Spatial and temporal heterogeneous trends of climate change (e.g., see Figs 3, 4 and 5) may constrain adaptive responses of birds to climate change. For instance, Finnish populations of Pied Flycatchers *Ficedula hypoleuca* are subjected to selective pressures favouring early-arriving individuals because of warming temperatures en route, while slight cooling at the beginning of reproduction in Finland have delayed hatching dates (Ahola et al. 2004, Laaksonen et al. 2006, Both and te Marvelde 2007). A similar case was detected in the Collared Flycatcher *Fycedula albicollis*, in which selection-mediated changes occurred at the genetic but not at the phenotypic level, being masked by concomitant opposite selection pressures (Merilä et al. 2001). This kind of situations may generate an evolutionary stasis having an apparent lack of adaptive response.

4.7 Conclusions

Understanding the relative roles of climate change experienced at different stages of the life-cycle is necessary to improve reliability of forecasting models, eventually driving conservation policies. In light of our results, the importance of temperature changes as driver of changes in bird migration needs to be critically tested and potentially revised. Others factors, like precipitation, food availability, habitat deterioration or changes in community structure must be taking into account.

5. Supplementary Tables

Printed versions of these tables are available in supplementary materials at the end of the volume. To access electronic version, click or copy and paste the following links in your browser.

Table S1
List of the 77 trans-Saharan species studied along with their migratory phenology, wintering season, mean breeding latitude.
https://dl.dropboxusercontent.com/u/22345958/SuppMat%20MM%20thesis/chapter%20III/Table%20S1.pdf

Table S2
Results of the general least square models carried out for each species. A: models run considered the short time frame (1 week) for each phenological period, B: models run considered the wide time frame (5 weeks). See Methods for details. https://dl.dropboxusercontent.com/u/22345958/SuppMat%20MM%20thesis/chapter%20III/TABLE%20S2.pdf

Annex 1
Complete list of the publications used to collect information about wintering events in Spain, Portugal and Morocco between 1969 and 2006. https://dl.dropboxusercontent.com/u/22345958/SuppMat%20MM%20thesis/Annex%201.pdf

CHAPTER IV

Rapid shortening of migratory distances of recently established wintering populations of trans-Saharan birds in the Western Mediterranean

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Unpublished Manuscript.

Abstract

In the last decades, European long distance migrants have established wintering populations north of the Sahara. This change in migratory behaviour is interpreted as an adaptive response to climate change. It is predicted that these populations will continue to progressively shorten their migration distance by moving their wintering area northwards, towards their breeding areas and become partially-migrant or sedentary. We tested this prediction by studying changes in the distribution of wintering records of trans-Saharan species in the Western Mediterranean between 1969 and 2006. Overall, the centre of abundance and the northern limit of the range of long-distance migrants wintering north of the Sahara shifted northwards 16.95 km/yr (n=56 species) and 8.39 km/yr (n=36 species), respectively. The centre of abundance also moved eastwards 6.05 km/yr, demonstrating a spread in northeastern direction. Strong selection for shorter migration may explain these observed rapid changes in the distribution of recently established wintering populations of long-distance migrants.

1. Introduction

In the last decades, organisms have shown notable changes in their population dynamics, distributions and life cycles in response to climate change (Parmesan 2006). Migratory birds are not an exception: advance of spring migration and breeding phenology have been reported for many populations from very different species (Lehikoinen and Sparks 2010, Knudsen et al. 2011). Based on mark-recapture methods (i.e. ringing), a reduction of migration distance has been found in many short to medium distance migrants (Fiedler 2003, van Vliet et al. 2009, Visser et al. 2009, Smallegange et al. 2010, Heath et al 2012). Moreover, long-term population censuses have demonstrated that non-breeding distributions have moved northwards as a possible response to climate change (La Sorte and Thompson 2007, Lehikoinen et al. 2013, Maclean et al . 2008). Finally, in the Blackcap (*Sylvia atricapilla*), a genetic driven reduction of migratory activity has been observed in a few generations (Pulido and Berthold 2010), suggesting that changes in migratory behaviour of birds may be attained by rapid microevolution.

Information for long-distance migrants out of the breeding season is generally scarce and consequently little is known about changes in migratory behaviour in this phase of the life cycle. Yet, in at least one species, the Barn swallow (*Hirundo rustica*), a progressive northward shift of the sub-Saharan wintering quarters has been described (Ambrosini et al. 2011). However, the Sahara desert is a barrier and progressive northward shifts of wintering distributions are constrained up to reaching the Sahel. The next step of this adaptive process would be a sudden change in the wintering areas by establishing populations north of the Sahara, i.e. in Mediterranean latitudes. Empirical evidence demonstrates that trans-Saharan migrants are being more frequently reported wintering north for the Sahara during the last years (Berthold 2002, Fiedler 2003, Chapters I and II). This evidence raises the question of whether a progressive northward shifting of the distribution is still under way for those populations that have established wintering populations north of the Sahara. The threshold model of migration predicts that under a selection regime favouring residency, the shortening of migration distance in long distance migrants should persist until the population becomes partially migratory or resident (Pulido 2007b, 2011). Therefore, a progressive northward shift of the new wintering grounds in the Mediterranean region is expected. Here, we have tested this prediction by analysing geographical changes between 1969 and 2006 in the distribution of wintering records of trans-Saharan species in the Western Mediterranean.

2. Methods

2.1 Wintering data

We collected all published winter records of trans-Saharan migrant species between 1969 and 2006 occurring in Spain, Portugal and Morocco (363 bibliographic references, complete list in Annex 1in Supplementary Materials at the end of the volume. Direct-link to electronic version: *https://dl.dropboxusercontent.com/u/22345958/SuppMat%20MM%20thesis/Annex%201.pdf*). A species-specific time window was defined for the wintering period to control for phenological differences in the migratory schedule among species and avoid any confusion with late or early migrants in autumn or spring, respectively [see details in Chapters I and II]. We considered only those wintering records with a precise location and number of observed individuals. A total of 6,213 records belonging to 80 species were available for the analyses.

2.2 Calculation of the parameters and potential biases

As first step, we selected only those species observed at least 10 years between 1969 and 2006, which reduced our dataset to 56 and 36 species for the centre of abundance and the northern edge analyses, respectively (see Supplementary Table S1).

For every species and year we calculated two different parameters describing the winter distribution: (1) geographical centre of abundance and (2) latitude of the northern edge of the distribution. Centre of abundance was derived as the average latitude and longitude weighted by the number of individuals observed in each record, considering the whole dataset. The northern edge of distributions was estimated as the 75th upper percentile of the distribution weighted by the number of individuals of each record. For the northern edge, we only considered records from the Iberian Peninsula. This selection was done because we considered that to describe movements of the northern edge of the wintering distribution was more relevant to explore only tendencies in the northern group of observations. Actually, we expected that by excluding Moroccan observations the sensibility of our analyses to potential latitude shifts would be enhanced. Moreover, by selecting data we aimed to control for the potential bias due to sampling effort. During the study period sampling effort increased as the number of birdwatchers in Spain, Portugal and Morocco increased. If the sampling effort do not have a homogeneous geographically increase, it may lead to a false increase of wintering records in those areas under the higher increase in the number of birdwatchers. To control for this potential bias, we analysed temporal trends in the number of the members of the Spanish Ornithological Society (SEO-Birdlife) in all Spanish provinces excluding Canary Island but including a part Ceuta and Melilla (N=50) between 1954 (year of foundation of SEO-Birdlife) and 2008 (most recent year of the available data). The geographic distribution of members of

SEO-Birdlife can be assumed confidently as a surrogate of the distribution of potential observers (i.e. birdwatchers) and thus, ultimately as a surrogate of the sampling effort invested in different areas and years. Temporal trends were tested by linear regressions. We found that the number of members of SEO-Birdlife increased in all the provinces during our study period (all positive coefficients and $p<0.05$, see Supplementary Table S2. We thus tested in a linear model if value of correlation coefficient expressing the increase of each province in the numbers of affiliated to SEO-Birdlife was depending on the mean latitude and/or longitude of the provinces. In none of the tested models these variables had a significant effect: model including only latitude [p=0.416]; only longitude [p=0.852]; both [Long. p=0.837, Lat. p=0.418]; both and their interaction term [Long. p=0.863, Lat. p=0.823, Long.*Lat. p=0.856]. Therefore, it can be concluded that the numbers of observers and consequently their sampling effort has increased homogeneously across Spain in the time window to which our observations belong to (1969-2006). Given that the most of the observations coming from Iberian Peninsula occurred in Spain, we considered this result as the best possible test to support that patterns of movements of northern edge of the wintering distribution are not affected by biases in the distribution of the observers. A second potential bias in our estimates of shifts in the new wintering Mediterranean areas of trans-Saharan birds could be the different length of the time-series, as well as differences in the starting and ending years of the time-series, for the geographical centres of abundance. For the latitudinal displacements, we found statistically significant associations between the rate of northward spread and the sample size (i.e., number of years with available data; r=-0.284, p=0.035), and the starting year of the time-series (r=0.319, p=0.017). The last year with records in the time-series had no significant effect (r=-0.164; p=0.231). Thus, the greatest rates of northward progression (i.e., positive slopes between latitude and year) were found in those species that have been recorded more recently and during less years wintering in the western Mediterranean. There are two possible causes for this pattern: 1) the northward progression is faster during the first years of the colonization, 2) the northward progression rates are being accelerated in recent years as environmental conditions promoting bird wintering in Mediterranean latitudes are becoming more favourable. Interestingly, we did not find any potential bias of time-series characteristics over longitudinal displacement rates (sample size: r=-0.060, p=0.659; starting year: r=-0.087, p=0.526; ending year: r=-0.259, p=0.054).

Finally, a third potential bias on data may be due to changes in population size of the bird species studied. One may hypothesize that probability of recording wintering individuals in the Mediterranean is higher when the population size is larger, i.e. the more individuals there are, the higher the probability of novel migratory behaviours. Therefore, the wintering geo-

graphical range may spread (e.g. northward progression) simply because population is becoming larger. This hypothesis is difficult to check because there are not yearly accurate annual estimates of the numbers of individuals composing Western European populations of the target species of this study. At most, is possible to test if the trend in the number of the trans-Saharan birds wintering in western Mediterranean is related to the population trends in Western Europe. In Chapter II, we tested this hypothesis in a sub-sample of 69 species. Those phylogentically-corrected analyses showed that population trends did not foresee at all the number of wintering events, ultimately suggesting that also the patterns studied in the present work are independent from yearly oscillation in population size.

2.3 Statistical analyses

We tested for temporal shifts in both parameters by linear regression with year as explanatory variable. The regression coefficients were transformed into kilometres-per-year units considering that 1° of latitude measure 111 km and 1° of longitude at 35° of latitude is 100.29 km. In all species, the absolute displacement recorded during the study period in its centre of abundance or northern edge was calculated as the product of the slope by the period with records.

The displacement (both as a rate and as the absolute value) of the centre of abundance of the wintering distribution of each species can be considered as a vector because there was a longitudinal (x) and latitudinal (y) component. Therefore, a vector with a certain length and angle can be calculated.

Length was obtained by applying the Pythagora's theorem:

$$\text{Vector length} = \sqrt{(\text{latitude shift}^2 + \text{longitude shift}^2)}$$

Vector direction (i.e. angle) was calculated as the inverse of the tangent of the quotient between the latitudinal shift (i.e. opposite leg) and the longitudinal shift (i.e. contiguous leg):

$$\text{Vector direction} = \arctan(\text{latitude shift} / \text{longitude shift})$$

The pairs of length and direction of species vectors were used to calculate a mean vector length and direction for the whole set of 56 species. The Hotelling's test was used to test whether the angles weighted by their lengths have a significant mean direction. The null hypothesis is that there is no mean direction.

3. Results

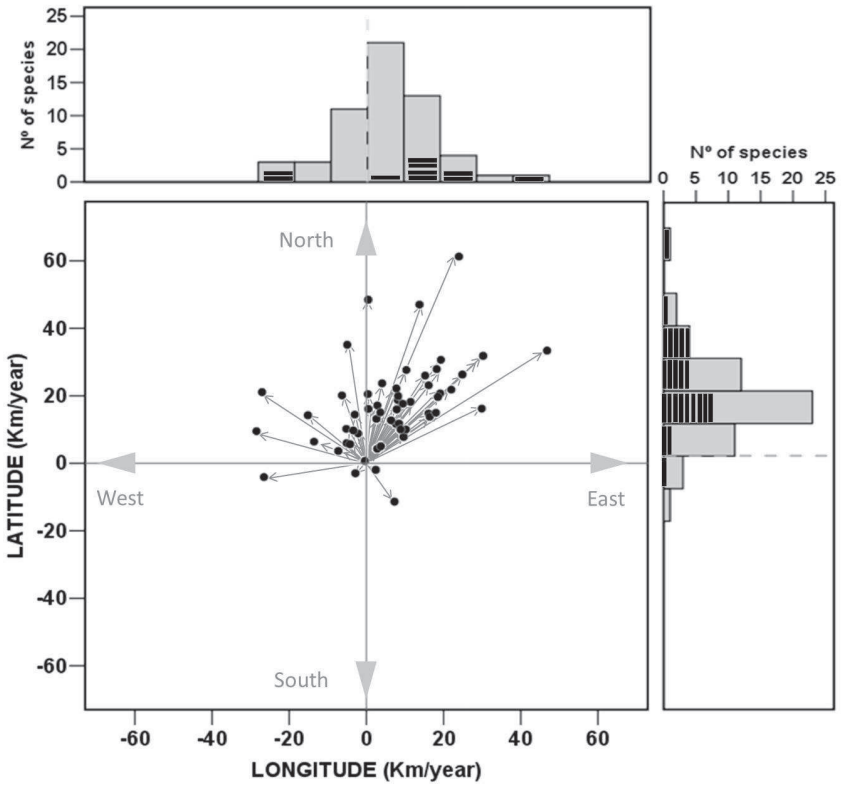
The centre of abundance of the winter distribution moved significantly northwards in 28 and eastwards in 10 out of 56 (Figure 1; Table S1). Overall, the mean vector of progression rate for the 56 species was 16.26 km/yr with an angle of 45.01° (0°=north, 90°=east etc.), i.e. with an almost perfect north-

east direction (Hotelling's Test: F=35.98, p<<0.001). On average, centre of abundance of winter distributions is moving 16.95 km/year (SD 12.57) northwards and 6.05 km/year (SD 15.10) eastwards. These rates of progression implied an absolute displacement of the centre of abundance for the 56 species following a vector of 480.3 km length and 46.91° (Hotelling's Test: F=39.67, p<<0.001), i.e. 485 km (SD 352) northwards and 187 km (SD 431) eastwards.

The northern edge of winter distributions moved significantly northwards in 16 out of 36 species (Figure 2; Table S1). Overall, the average progression rate was 8.39 km/yr toward the north (SD 10.56; t-test against 0: t_{35}=4.76, p<0.001), which implied an absolute northward displacement of 215 km (SD 283) of the northern edge during the study period in the 36 considered species.

Figure 1

Species vectors for the progression rate of the centre of abundance of the recently established wintering areas in the Western Mediterranean. Histograms show the distribution of the latitudinal and longitudinal shift rates. In black shifts with p < 0.05.



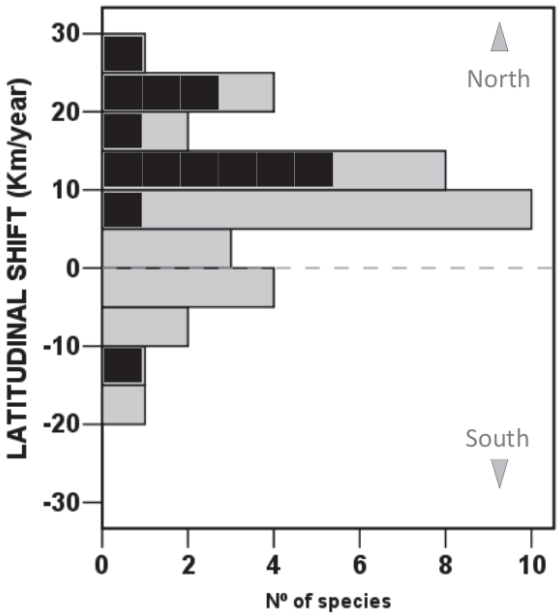


Figure 2
Distribution of latitudinal shift rates of the northern edge of the wintering distribution. In black shifts with $p < 0.05$.

4. Discussion

We have found that once trans-Saharan species succeed in establishing wintering populations north of the Sahara (Chapter II), these populations continue spreading northwards. This shift may be resulting in a shortening of migration because distance between wintering and breeding areas is progressively reduced. This adaptive response is expected in migratory species under a climate change scenario (Pulido 2007b, Pulido and Berthold 2010, Coppack et al. 2003 and 2008), but this phenomenon had only been reported hitherto for short and middle-distance migrants (La Sorte and Thompson 2007, Maclean et al. 2008, Visser et al. 2009, Smallegange et al. 2010, Heath et al. 2012, Lehikoinen et al. 2013; but see Ambrosini et al. 2011).

Pulido and Berthold (2004) predicted that long-distance migrants would only be able to evolve towards residency if they succeeded in establishing populations north of ecological barriers (e.g. the Sahara Desert) located between the breeding and wintering areas. A large proportion of trans-Saharan species has been indeed able to do so in recent decades (Chapters I and II). Moreover, they continue shifting north their wintering range according to predictions, as we have demonstrated here. This fact supports the hypothesis that selection favouring a shorter migration distance, and ultimately residency, has

been ongoing between 1969 and 2006 in Western European migratory bird populations. We predict that, if selection for shortening migration persist, as expected under future climate scenarios (Pulido and Berthold 2004, Pulido 2007b), this process will rapidly result in the evolution of partial migration and residency. To date, this has only been demonstrated in a completely migratory blackcap population (Pulido and Berthold 2010), but our study provides empirical evidence that adaptive change from long-distance migration to residency is also happening in a wide sort of trans-Saharan species. This phenomenon has been traditionally neglected (Knudsen et al. 2011), but changes of the wintering areas may be more common than expected in long-distance migrants too.

All parameters describing shifts of the winter distribution showed marked variability among species. Such variability could be due to different intensity of the selective pressures acting at the specific level (e.g. populations subjected to different degree of climate change in their breeding areas), as well as to different adaptive capacity of each species (Gordo and Doi 2012). Indeed, despite our study suggests an ongoing adaptive change of migratory behaviour in European long-distance migrants, it must be noted that the evolution towards residency is not happening in all species. Out of the 80 species recorded, only 56 were observed more than 10 years to assume that they are regularly wintering north of the Sahara. The other 24 seems unable to establish wintering populations in Mediterranean latitudes. Ecological and physiological constraints are likely to hamper the adaptive capacity of these species (Coppack and Pulido 2004). Moreover, most of these are also suffering declines attributable to climate change (Both et al. 2006, Møller et al. 2008, Saino et al. 2011), so populations of these species may lack of enough variance in migratory behaviour to show any adaptive response at all (e.g. Gordo and Doi 2012).

5. Supplementary Tables

Printed versions of these tables are available in supplementary materials at the end of the volume. To access electronic version, click or copy and paste the following links in your browser.

Table S1 (Chapter IV)
List of trans-Saharan species studied and their results for the centre of abundance and northern edge of their recently established wintering areas in the western Mediterranean. For both parameters the number (n), the first and the last years with winter occurrences of the species are shown. For the centre of abundance, results from linear regressions between latitude and longitude centres with year are shown as the regression coefficients (slopes), correlation coefficients (r), and p-values (p). Positive slopes mean northward or eastward, respectively, displacements. These pairs of slopes were used to calculate a vector and angle to estimate the direction and rate of displacement of the centre of abundance. Absolute displacement in latitude and longitude attained during the period with available data for each species are also shown, as well as its derivate vector. For the northern edge, results from linear regressions between latitude of the 75th percentile of data and year are shown as the regression coefficients (slopes), correlation coefficients (r), and p-values (p). Positive slopes mean northward displacement. The absolute displacement is also shown.

Direct link:
https://dl.dropboxusercontent.com/u/22345958/SuppMat%20MM%20thesis/chapter%20IV/TABLE%20S1_IV.pdf

Table S2 (Chapter IV)
List of the Spanish provinces for which correlation between number of members of SEO-Birdlife and year was tested (r= Pearson's correlation coefficient). P values are given in scientific notation. Mean latitude and longitude of each province is also shown.

Direct link:
https://dl.dropboxusercontent.com/u/22345958/SuppMat%20MM%20thesis/chapter%20IV/TABLE%20S2_IV.pdf

Section II

Insights from partially-migrant Iberian Blackcaps

Adult female 2N93692 take a break on a poplar branch nearby the kaki trees where she's fighting for her access to the fruit that guarantee her winter survival.

CHAPTER V

Complete post-juvenile moult in first-year Blackcaps: proximate causes and adaptive implications

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Abstract

Moult is one of the most energy-demanding events in the annual cycle of a migratory bird. As a consequence, moult patterns have evolved that separate moult from other costly life-cycle stages and that exclude unnecessary replacement of the feathers. We studied two Spanish blackcap *Sylvia atricapilla* populations with the aim of elucidating variation and flexibility of their postjuvenile moult pattern. In contrast to most juveniles of this species, which normally undergo a partial moult both in captivity and in the wild, we found complete moult in 2 juvenile blackcaps. Complete moult was also inferred for another 7 birds, which were in active moult. Eight of these birds were trapped at a site in northern Spain and one originated from a partially migratory population from eastern Spain. This bird, held under the same environmental conditions as other 31 juveniles from the same population, moulted all primaries in captivity while the other 31 juveniles invariably undertook a normal partial post-juvenile moult. Therefore, it seems likely that complete post-juvenile moult observed in this bird was not induced by environmental conditions but had a genetic basis. Thus, we show that previously undetected variation among post-juvenile moult patterns is present in wild blackcaps and suggest that variation in the expression of important life-history traits could represent a potential reservoir for adaptive changes. This finding is in line with the great adaptive capacity of blackcap, repeatedly observed both in wild and in captivity.

1. Introduction

Life-history theory predicts that life-cycle events should be scheduled in a way that the total fitness of the individual is maximised (Roff 2002). One way of maximising fitness is to temporally separate events in the lifecycle that demand large amounts of resources. For birds, the most important and energy demanding life-history stages are: reproduction, moult and, when it occurs, migration (Newton 2008 and 2009). As a consequence, we expect birds to maximize their fitness over the complete life-cycle by optimal scheduling of reproduction, moult and migration (Barta et al. 2006 and 2008, Hedenström et al. 2007, McNamara and Houston 2008). Moult is costly both because of high energetic and nutritional demands during feather synthesis (Murphy and King 1992, Lindström et al. 1993, Murphy 1996 and 1999) and because of reduced thermoregulation efficiency and aerodynamics of plumage during moult (see, for instance, Schieltz and Murphy 1997, Swaddle and Witter 1997, Hedenström and Sunada 1999, Guillemette et al. 2007). Annual-routine models have been used to investigate whether different patterns of moult should evolve in birds differing in migration strategy (Barta et al. 2006, McNamara and Houston 2008). They suggest that there is an optimal moult pattern for each migration strategy. Specifically, these models predict that migrants would gain a maximum benefit from a rigidly programmed moult schedule, while in residents a more flexible organization of life-cycle events is expected. Moreover, an overlap between renewal of primaries and reproduction is predicted to be the optimal strategy only for birds living in habitats with low seasonality, for example, in the tropics (Barta et al. 2006, McNamara and Houston 2008). In nature, however, it also has been observed in extreme northern breeders. In these birds, which stay only few weeks in the breeding quarters, the overlap between reproduction and primary moult is supposed to be an adaptation to time constraints. In most cases, deviations between predicted optimal moult strategies and actual moult patterns are probably due to the fact that a strategy is optimal only under very specific conditions and for a very specific group of birds. In passerines, for example, moult strategies generally differ between juvenile and adult birds (Jenny and Winkler 1994). Since the energetic costs of moult increase with the extension of moult, we would expect strong selection against unnecessary replacement of the plumage. This probably explains why the general moult pattern among Western Palearctic short-distance migrants is characterised by a partial moult in the first summer of life and a complete moult (i.e. renewal of all the feathers, including the primaries) in following years (Jenni and Winkler 1994). In late summer, i.e. between reproduction and migration, the feathers of juveniles are only a few weeks old, while the primaries of adults were grown in the previous year and are worn. Therefore,

it seems adaptive that juveniles do not renew the wing feathers while adults do. Nevertheless, this is not a general rule because the extent of juvenile moult may vary considerably among different species (Svensson 1992, Jenni and Winkler 1994). This may partly be due to phylogenetic constraints on the evolution of moult patterns (Svensson and Hedenström 1999, Hall and Tullberg 2004). Phylogenetic constraints on moult pattern variation are consistent with the general finding that phenotypic variation in moult is to a large extent due to genetic differences (Berthold and Querner 1982, Pulido and Coppack 2004, I. de la Hera et al. pers. obs.). One of the model groups for studying the evolution of variation in moult patterns are the Western Palearctic warblers of the family Sylviidae (Svensson and Hedenström 1999, Hall and Tullberg 2004) and among these, particularly, the *Sylvia* warblers (Shirihai et al. 2001). The blackcap *Sylvia atricapilla* has been particularly well studied both in captivity and in the wild (Berthold and Querner 1982, Norman 1990; Berthold et al. 1990 and 1994; Herremans 1991, Shirihai et al. 2001; Pulido and Coppack 2004). In this species throughout the whole breeding range and within each subspecies, partial moult among juveniles and complete moult among adults at the end of the breeding season are the rule (Shirihai et al. 2001). Yet the extent of partial post-juvenile moult may vary both within and among populations, being generally more extensive in southern populations (Jenni and Winkler 1994). Exceptionally, juvenile blackcaps may also show moult of some external primaries and/or inner secondaries (Shirihai et al. 2001; Blasco-Zumeta 2012). Here we use moult data derived from a long-term field study and from a common garden experiment on Spanish blackcaps to draw inferences on the mechanism controlling the occurrence of rare moult patterns and to discuss possible implications for adaptive evolution of this species, particularly in response to climate change. For the first time, we report complete juvenile moult in the blackcap, and discuss its potential control and maintenance.

2. Methods

2.1 Common garden experiment

During the breeding seasons 2010 and 2011, we collected 31 first-year blackcaps from a partially migratory population in eastern Spain, Cocentaina (38º 44' N - 0º 44' W, province of Alicante) and transported them to our experimental facilities in the Casa de Campo, Madrid (40º 25' N; 3º 42' W). This was part of a larger experiment, which aims at studying within and among-population differences in migratory behaviour and life histories in Iberian blackcap populations (Pulido et al., 2011). Our specific experimental cohort was composed of birds taken as chicks from their nest when 7-8 days old (N = 9) or captured as fledglings in

their first plumage during the late breeding season (N = 22). As of the date of collection, all birds were maintained under the same environmental conditions (i.e. ad libitum food and water) exposed to the natural light regime of Madrid, Spain. In the following weeks, we determined individual moult status by quantifying the number of growing feathers both in wings and body. For birds from the 2010 cohort, this was done on September 9, while in 2011 this was done on September 7 and repeated on September 24th. This common-garden experiment, which minimised among-individual environmental variation, allowed us to study the causes underlying potential differences in moult patterns. In this experiment, all birds experienced identical environmental conditions (e.g. light period, temperature, food, social interactions). As a consequence, any potential phenotypic difference observed must have had other causes (e.g. genetic differences, differences in maternal effects, differences in the environment experienced before collection). Although captive conditions have been reported as potentially affecting moult (i.e. duration of moult in ducks, Butler and McGraw 2009), to the best of our knowledge, there is no evidence suggesting that captivity may affect moult extension or "type" (i.e. considering complete versus partial moult). Feathers numbers in the text are assigned in descendent order (see, Jenni and Winkler 1994).

2.2 Wild

In order to compare moult extension between birds from the same population studied in captivity and in the wild, we captured and determined the number of renewed feathers in 43 first-year blackcaps from Cocentaina during the breeding seasons (April-August) 2010 and 2011. Age determination in this sample of birds was based exclusively on common plumage observation criteria (Svensson 1992, Jenni and Winkler 1994), which cannot identify first-year birds that undertook complete moult in the previous summer. Therefore, we cannot rule out that juvenile birds with complete moult were overlooked. With regard to migratory behaviour, this population is considered as partially migratory (Morganti et al. 2012). The other population investigated was located in the Natural Park of Garaio (42º 54' N 2º 32' W, province of Alava, northern Spain). Between 1994 and 2009, 1,726 blackcaps were captured at the local constant- effort ringing station. We obtained information on the extension of moult for 486 of these birds, which were in their first year of life. In this population, birds were aged by the combination of common plumage observation criteria and observation of cranial ossification (Jenni and Winkler 1994). This population is likely to be completely migratory since there are no winter captures of individuals breeding at this site (Onrubia et al. 2012). Further evidence for the migratory status of this blackcap population comes from recoveries of breeding birds in winter: two breeders from this population were recaptured

in the Ebro Valley area, c.a. 200 km south-west to the breeding site and two individuals in north Africa (one in Morocco and other in Algeria, A. Onrubia et al. pers. obs.).

2.3 Statistical analyses

We compared moult extension in wild and lab cohorts by computing a chi-square test for each group of feathers (great coverts GC, primary coverts PC, bastard wing BW, carpal feather CC, tertiaries TER). For PC we perform the test using the frequencies of birds that do not renew any feather of the group. Obviously, we excluded birds with complete moult from analyses. Using Pearson's correlations, we tested whether the number of new and old feathers among the eight wild birds captured in Garaio was related to Julian date.

3. Results

3.1 Cocentaina birds in captivity *(common-garden experiment results)*

All birds from both cohorts (2010 and 2011) were actively moulting body plumage when studied at the beginning of September. At this time, moult of greater, median and primary coverts, of the bastard wing and carpal feathers were already completed, so that we could measure the extension of partial moult considering these groups of feathers. Most of the birds (90.6%) renewed all the greater coverts and one or two bastard wing feathers. About half of the birds also renewed the carpal feather. Only one bird renewed some primary coverts and none renewed all of them (see Figure 1). One male from the 2011 cohort, checked on the 7 September 2011, was apparently undergoing a complete moult, including all the wing feathers, retaining only PC 4 to 9 (see Figure 2 for details on the status of the moult). On the 24th September, we checked this bird again. The inspection of wing feathers corroborated that this bird was undergoing a complete moult and that at this date it was almost completed, except for inner secondaries that were almost grown (left wing: S6 and S5 status 4; right wing: S6 status 4, S5 and 4 status 3). Data about this bird's migratory restlessness show that the bird had started its preliminary night restlessness on 13th September, and had developed a consistent "migratory activity" in the next few days.

3.2 Wild

3.2.1 Cocentaina

Wild birds (N = 43) presented a moult pattern that did not statistically differ from to the one shown among experimental birds (Chi-Square tests. GC: $\chi^2_1 = 0.43$, p = 0.51; CC: $\chi^2_1 = 0.04$, p = 0.89; PC: $\chi^2_1 = 0.01$, p = 0.92; BW: $\chi^2_1 = 0.44$, p = 0.51; TER: $\chi^2_1 = 0.19$, p = 0.66) (Figure 1). The lack of significant differences between moult extension in experimental and wild birds suggests that birds in captivity moulted normally, so that patterns observed among these birds are representative of birds in the wild. Considering the

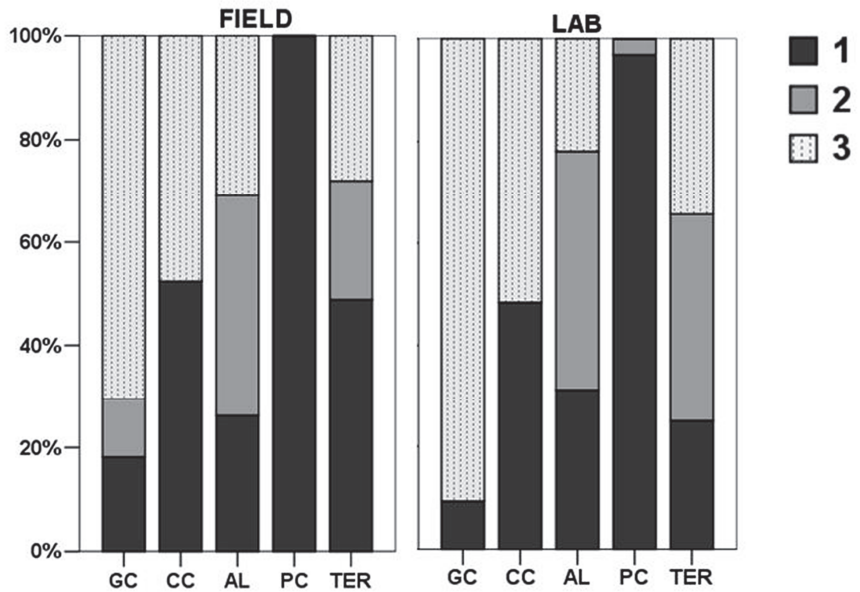
whole cohort from Cocentaina pooled (both lab and wild birds), only one out of 74 birds (1.35%), showed complete juvenile moult.

3.2.2 Garaio

In this locality we captured seven juvenile blackcaps in active primary moult. They were identified as "juveniles" from the aspect of the plumage not yet moulted (also the "old" feathers appearing fresh) and by incomplete cranial ossification (following Jenni and Winkler 1994). A further bird was captured with a completely renewed plumage and classified as "juvenile" by its still incomplete cranial ossification (score 4). Since passerines complete skull ossification within few months of life, we can infer that this bird was born that year and was only a few weeks old. These eight birds were captured between August and October in four different years: 1998 (1 individual), 1999 (1 individual), 2001 (4 individuals)

Figure 1

Extension of post-juvenile moult in the population of Cocentaina (Alicante, eastern Spain). The two groups represent wild (N = 43) and experimental (N = 31) birds. Bars represent different groups of feathers. GC: great coverts; BW: bastard wing; CC: carpal feather; PC: primary coverts; TER: tertiaries. 1: all feathers of the group remain unmoulted; 2: some of the feathers of the group new and some old; 3: all feathers of the group renewed. Only for GC 1: one or two retained, 2: three or four retained, 3: all renewed.



and 2003 (2 individuals). (see table 1 for a complete list with details and raw data on moult status). We assume that all these birds were born locally because (1) the capture date for six of these birds lies outside the established time window for migration of blackcaps at Garaio (15 Sept-31 Oct; Onrubia et al. 1996), (2) all birds, except one, had a wing length below 75 mm, resembling local breeders, but unlike birds that migrate through the area, which tend to have longer wings, and (3) because of all the birds had low or missing fat deposits (fat-scores 0 or 1 following Kaiser's 1993 classification). These birds showed a significant correlation between capture date and progression of moult (new feathers: r = 0.913, p = 0.002; old feathers: r = –0.939, p = 0.002; n = 8, see Figure 3), supporting the idea that all seven complete moult. Further support for this idea comes from the fact that these birds were moulting primaries in the normal progression as at the start of complete moult process (from inner to outer primaries), while juveniles with accidentally moulted primaries are normally renewing the external ones (Jenni and Winkler 1994; Shirihai et al. 2001). The percentage of juvenile birds showing complete or active moult of inner primaries in Garaio was 1.65% (8 out of 486), which does not statistically differ from the frequency observed in the Cocentaina population ($\chi^2_1 = 0.03$, p = 0.85).

Figure 2

Moult status on 7th September 2011 of the captive first-year male showing complete postjuvenile moult (except for PCs 4 to 9 and right P10). The male belongs to the partially migratory population of Cocentaina (Alicante, eastern Spain), and was kept under controlled environmental conditions in captivity. Colours represent the 0 to 5 categories described in Ginn and Melville (1983) with 0 meaning an old feather, 5 a complete grown new one and intermediate numbers meaning progressively more advanced growing stadium. Feathers scored with 4 and 5 can be considered fully functionally to flight. By 24th September 2011 almost all the wing feathers except for few secondaries were fully grown and renewed. Wing shape modified from Blasco-Zumeta (2012).

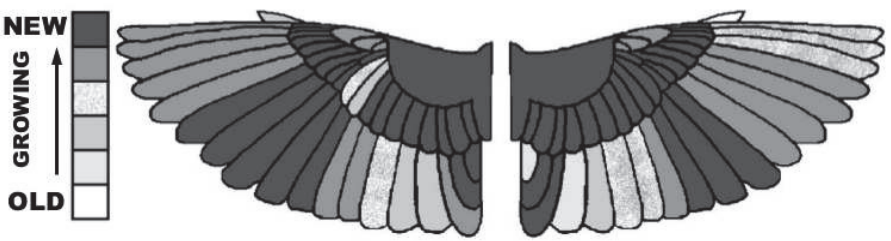


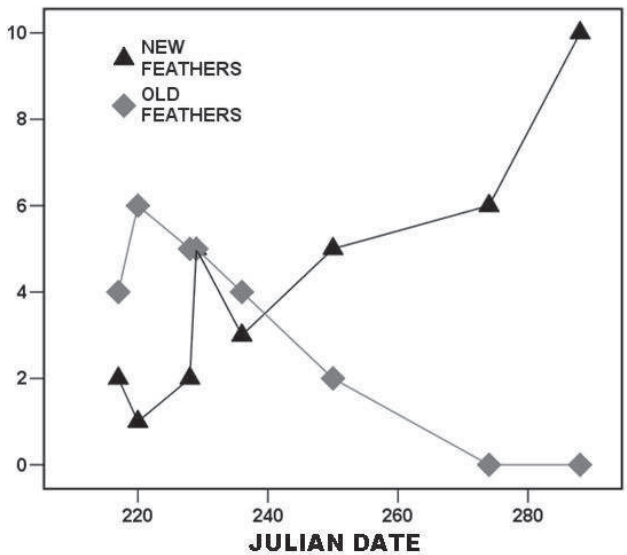
Table 1

List of first-year birds captured in active primary moult at Garaio (Alava, northern Spain). All birds were aged by observation of the contrast between moulting and un-moulted feathers and/or by cranial ossification status (codes ranging from 0 in nestlings to 7 in full adults; Jenny and Winkler, 1994). For each bird, raw data showing the moult progression for primaries is given. Primaries are ordered descendantly and codes means different status of growing from 0 (old feather) to 5 (new feather) following Ginn and Melville (1983).

Month	Day	Year	Sex	Body moult	Primary moult	Primary status (P1 to P10)	Skull ossification
August	4	2001	♂	Localized	Active	5543210000	2
August	7	1999	Unknown	Extensive	Active	5421000000	2
August	15	1998	Unknown	Extensive	Active	5543100000	3
August	16	2003	♂	Extensive	Active	5543100000	2
August	23	2001	♂	Extensive	Active	5554310000	3
September	6	2003	♀	Extensive	Active	5555543100	2
September	30	2001	♂	Completed	Active	5555554321	4
October	14	2001	♀	Completed	Completed	5555555555	4

Figure 3

Moult progression in the 8 wild birds captured in Garaio (Alava, Spain) between 1998 and 2003. Black triangles show numbers of completely grown feathers while empty square show numbers of feathers of the previous generation (i.e. first plumage feathers). Day 220 corresponds to 8thAugust in non-leap years.



4. Discussion

Our study suggests that a small proportion of Spanish blackcaps undergo a complete post-juvenile moult. This moult pattern found at low frequencies in two different Spanish populations, was not environmentally determined, as demonstrated in our common garden experiment, but is likely to have a genetic basis.

4.1 Frequency and geographic distribution of complete juvenile moult in the blackcap

Generally, juvenile blackcaps moult 3-10 great coverts (50% of the juveniles renew 10). The bastard wing generally remains un-moulted, or with a single feather renewed (c.a 30% of the cases). Two to three tertial feathers are renewed. The carpal feather, the primary coverts and the tail feathers are only seldom renewed (less than 10% of the cases) (Jenni and Winkler, 1994; Shirihai et al., 2001). Exceptionally, juvenile blackcaps may also show moult of external primaries and/or inner secondaries (0.2% out of 1,891 individuals, Shirihai et al. 2001). Despite the large amount of studies on captive birds, complete juvenile moult in blackcaps has not been previously observed. Berthold et al. (1990) reported post-juvenile moult extension based on about 2,000 juveniles in southern German blackcaps held in captivity between 1968 and 1970. They found 2% of these birds showing a moult that included all tertiaries and the inner secondary, but they never observed a single bird with a complete moult. However, Berthold et al. (1990) did not consider blackcaps of southern Europe in their study. Likewise, Shirihai et al. (2001) did not report any complete moult among juvenile blackcaps, although mostly they studied birds from the Mediterranean area (about 2,000 birds from NE Spain). To our knowledge, the most extensive juvenile moult hitherto reported in blackcaps are birds moulting 1 to 5 external primaries and 1 to 3 inner secondaries (Shirirai et al. 2001, Blasco-Zumeta 2012). This study is the first report of juvenile blackcaps moulting inner primaries and, for one population at least, we could demonstrate that the progression of moult observed in the wild is in the right chronological order expected for a complete moult. This strongly suggests that this moult pattern is a rare but regular phenomenon in Iberian populations. In general, it is very likely that the incidence of complete post-juvenile moult in blackcaps (and other species) is higher than reported here, since the method for ageing birds is based on the assumption that juvenile blackcaps do not undergo a complete moult, and systematic check of cranial ossification is done at very few ringing stations. A juvenile bird is normally identified by the presence of feathers from different generations in the wing. Therefore, juveniles that conducted a full moult will be considered adults and remain undetected. Apart from birds captured in first plumage and maintained in captivity, only data from constant effort sites with high numbers of recaptures between seasons could detect such

unusual moult patterns. This is corroborated by the fact that at the same site in northern Spain (Natural Park of Garaio, see above), where we found first evidence for juvenile blackcaps moulting full plumage, the first juvenile Cetti's warbler Cettia cetti with complete moult was detected (A. Onrubia et al., pers. obs.). The fact that all blackcaps with complete juvenile moult are from southern populations is in line with a general pattern found in European Passerines, i.e. that birds from southern populations have a more extended moult (e.g. Gargallo and Clarabuch 1995, and see Jenny and Winkler 1994). An adaptive explanation for this pattern could be that in southern European populations conditions at the breeding sites remain favourable during a longer time than in the north. As a consequence, the cost of replacing flight feathers in juveniles is probably lower in the south. At higher latitudes, birds have to leave the breeding areas early and endure long migratory flights. If the extent of moult is controlled by these selection factors, recent environmental changes observed in Europe and elsewhere, which involve a lengthening of the growing season (Menzel and Fabian 1999, Linderhölm 2006), could lead to an increase of the frequency of complete moult among first-year passerines.

4.2 Control of moult extent in the captive bird: genetic or environmental factors?

Intraspecific variation in the extent of postjuvenile moult is also found in other species of the genus Sylvia. It is especially variable in the sardinian warbler Sylvia melanocephala, in which early-hatched birds have a more extensive moult, which may be complete in some cases (Gauci and Sultana 1979). This pattern was also observed in other passerines belonging to the Turdidae, Paridae and Fringillidae (Noskov et al. 1999, Bojarinova et al. 1999), suggesting that hatching date is an important determinant of moult extension. For the blackcaps with complete juvenile moult described in our study, the hatching date is only known for the bird studied in captivity. This bird, however, could be considered as born late in the season (birth date: 7th June, 2011, the median hatching date for 9 nests from the same population in 2011: 28th May), which makes it unlikely that hatching date is the explanation for complete moult in this blackcap. Environmental conditions experienced by individual birds, and conditions experienced in captivity, are known to affect the speed of the moult in ducks (Butler and McGraw 2009). Therefore, in principle, it would be possible that conditions experienced by blackcaps in captivity could induce complete moult. However, we have no reason to assume that this was the case with the blackcap from Cocentaina, which had a complete juvenile moult. There is strong evidence that captivity does not influence the extent of moult (i.e. number of feathers moulted), as our data show (Figure 1), as other studies on blackcaps demonstrate (Berthold et al. 1990), and as reported for non-passerine species (Cieslak and Kwiecinski 2009). Moult extent was normal in all bird that we held in

captivity. The high moult intensity (6 and 7 primaries in active moult) found in the juvenile bird with complete moult is only slightly higher than the one that we registered for adults captured in active complete moult in the same population (mean number of primaries active moulting: 4, N = 3, our pers. obs.). Moreover, it has to be considered that feathers with even a minimum trace of the "waxy sheath" (defined in Ginn and Melville 1983) were scored as "in moult" even if they were fully grown and fully functional. Thus, we can consider the high moult intensity found in the juvenile blackcap held in captivity consistent with moult intensities in the wild. We can also exclude that physical condition may have induced complete moult: the bird undergoing complete moult presented good physical conditions (fat score: 1; muscle score: 2; weight: 17.31g), similar to that shown by the other experimental birds measured on the same date (median fat score: 1; median muscle score: 2; mean body mass ± C.I. 95%: 16.72 g ± 0.39, N = 20). The above mentioned evidences allow us to largely exclude environmental or physical conditions as causes of the observed moult pattern, endogenous genetic control remaining as the best explication for the observed phenomenon. Since we can exclude that environmental effects induced complete moult in the blackcap held in captivity, we need to infer other possible causes for the difference in the extent of moult found among individuals held in captivity. In principle, there are three possible explanations for the differences found in the common-garden experiment: (1) genetic effects, (2) maternal effects and (3) early common-environment effects (in the specific case, before the age of 8 days). Unfortunately, our experiment does not allow distinguishing between these factors. However, in view of other studies demonstrating additive genetic effects on winter moult extent (de la Hera et al., pers.obs.), and on the timing and duration of postjuvenile moult (e.g. Gwinner and Neusser 1985, Helm and Gwinner 1999, Pulido and Coppack 2004), and no evidence (Larsson 1996), we think that it is likely that the extent of moult is genetically controlled.

5. Conclusions

A main implication of this study is that previously undetected genetic and phenotypic variation in a life-history trait may exist in wild blackcap populations. If this variation is not phenotypically expressed (cryptic variation) it could be due in part to rare recessive alleles or, alternatively, to "genetic assimilation" (i.e. the expression of variation only under particular environmental conditions). Clearly, this unexpressed variation is difficult to detect and will largely remain undetected. Because genetic variance is the prerequisite for adaptive evolution (Falconer and Mackay 1996), the knowledge of existing genetic variability among traits gives a measure

of the extent of the adaptive potential of a species (i.e. blackcap) or population. We hypothesise that in blackcap populations, not only juvenile moult patterns, but many other traits, may show undetected phenotypic and genetic variation at low frequencies, producing a great extent of adaptive potential. This hypothesis is in line with the large potential of blackcaps for rapid evolutionary change (Berthold et al. 1992, Pulido and Berthold 2003, Bearhop et al. 2005, Pulido and Berthold 2010). If moult represents "a changeable event playing the part of the buffer in the annual cycle" (Noskov et al. 1999), the existence of variation in this trait could be particularly important for the adaptation to novel environmental conditions. Apart from describing a new pattern of moult in the blackcap, our results are an example of previously undetected phenotypic variation present at low frequency in wild populations of birds. This variation may be crucial for populations to adapt to rapid environmental changes. Specifically, we expect that changes in selection regimes due to climate warming will favour individuals having a complete postjuvenile moult. Thus, we predict that the frequency of this moult pattern in blackcaps will increase.

CHAPTER VI

Discrimination of residents and migrants by morphology and stable isotopes in a partially migratory Blackcap population

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Unpublished manuscript.

Abstract

Natural selection shapes the flight morphology of birds in relation to their migratory habits. Thus, conspecifics that differ in migratory behaviour but live in sympatry often can be identified by differences in their morphology. However, it is poorly explored if natural selection shapes different flight morphologies between the migratory and resident fraction of the same population of partial migrants. We approached these questions by studying Blackcaps (*Sylvia atricapilla)* from a study site where three categories of birds were found: all-year resident (R), migrants that breed in the area but spend their winter elsewhere (M), and migrants from other breeding populations that winter in the area (W). Individuals were assigned to each category according to their capture-recapture histories. We explored morphological differences in flight-related traits between these groups by using discriminant analyses. We also analysed deuterium (δD) in claws and feathers of M and R birds as an additional distinction method. Discriminant functions successfully distinguished over 80% of the sympatrically wintering birds (W vs R), but failed to discern between residents and migrants from the local partially migratory population. In addition, M and R did not differ in isotopic profiles. Our findings confirm the association between flight morphology and migratory behaviour, as found in R versus W Blackcaps, but shows that only a site-specific discriminant function can disclose this difference. The lack of differences between M and R birds in morphological and isotopic profiles suggests that the determination of individual migratory status in a partially migratory population is largely state-dependent. If migration occurs, it is probably performed over short distances. This interpretation is in accord with recent field evidence and theoretical models on partial migration control. Based on these findings, we call for the further exploration of the factors controlling the occurrence of partially migratory behaviour.

1. Introduction

Natural selection shapes behavioural and morphological traits in response to the ecological factors determining the life cycles of animals. In birds, flight-related morphology is largely associated to migratory behaviour (Leisler and Winkler 2003). Contrasting selective pressures that favour rounded wings, which improve manoeuvrability, or pointed wings, which are more suited for long-distance flights, are responsible for a large range of morphologies among different species of birds. Especially interesting from an evolutionary perspective are morphological differences between sister species that have recently diverged (Jahn et al. 2010a) or within species, in which populations differing in migratory behaviour may show different morphologies (Fiedler 2005, Milá 2008, Neto et al. 2013). In general, sedentary birds tend to have shorter, more rounded wings, larger tails and body size in relation to wing span when compared to their migratory conspecifics (Hedenström 2008, Milá et al. 2008). Blackcaps (*Sylvia atricapilla)* are a suitable model for studying the association of morphology and migratory behaviour because they have an exceptional variation of migratory phenotypes. Actually, populations of all degrees of migratoriness, from completely sedentary to long-distance migrants, may co-occur in small geographic areas (Cramp 1992, Shirihai et al. 2001). Previous studies demonstrated that flight morphology strongly differs between Blackcaps of different breeding origin and migratory habits (Fiedler 2005). Morphological differences between different breeding populations emerge not only when comparing populations far distant from each other, but even comparing populations from different regions within the Iberian Peninsula (Tellería and Carbonell 1999, de la Hera et al. 2007).

In Spain, the Blackcap is a common breeder (Martí and del Moral 2004), but also an extremely abundant migrant and wintering species (SEO/Birdlife 2012a). Morphological discrimination has been successfully used to identify migratory and sedentary individuals from Spanish sympatric populations both in winter and during the migratory season (Pérez-Tris et al. 1999 and 2001; Pérez-Tris and Tellería 2002; de la Hera et al. 2007 and 2012, Arizaga et al. 2012). Since migratory Blackcaps from different geographic areas may migrate along different flyways and use different wintering areas (Arizaga et al. 2012), it is likely to seriously limit the power of the discriminant function obtained at a specific study site and period, if applied to different study systems. In particular, discriminant functions were mainly estimated having as reference a resident population of Blackcaps from the southernmost point of Spain (Campo de Gibraltar: 36°15'N, 5°31''W), a site in which fossil evidence indicates that the species was present during glaciations (see references in Pérez-Tris and Tellería 2001 and Pérez-Tris et al. 2004). Thus, this "ancient" population of resident individuals has had a long time-span to adapt morphology to its resident behaviour. Morphological traits in birds from this population allow discrimination not only from

northern European migrants, but also from migratory conspecifics from northern Spain (de la Hera et al. 2007). During the warming period after the last glaciation, Blackcaps probably colonized Europe from this southern refuge by progressive establishing migratory populations at gradually more northern latitudes (Pérez-Tris et al 2004). These migratory populations may have become partially migratory and resident in only a few generations (e.g. Pulido and Berthold 2010), but it is unknown if morphology could adapt at the same rate. Partially migratory behaviour has been demonstrated in a Blackcap population in southern France (Berthold 1986). Yet, it is assumed that others coastal populations may are partiallly migratory too (e.g. Shirirai et al. 2001), which would render them a most suitable system to study the covariation between morphology and migratory behaviour. This covariation has special interest when applied to the study of non-breeding partial migration, i.e. systems in which part of the reproductive cohort leaves the site during winter (Chapman et al. 2011) because of its implications in the control of partial migration. Within-population morphology differences between resident and migrant individuals would be necessarily genetically determined and maintained through assortative mating. Consequently, such a finding would strongly support a genetic control of partially migratory behaviour. However, morphological differences between the sedentary and migratory fraction of a partially migratory population are more likely to be small, or absent in most cases (e.g. Fudickar et al. 2013), especially if the migratory behaviour is linked to dominance hierarchies and/or environmental oscillations (Pulido 2011). Given that this eventuality is considered to be the most common framework in which partial migration occurs (Pulido 2011), other evidence demonstrating partially migratory behaviour, in addition to capture-recapture histories, is needed. Isotopic signature (especially δD) is one of these evidences, as it had been shown to be a powerful tool to distinguish resident from northern immigrant Blackcaps (de la Hera et al. 2012), but also to distinguish Blackcaps from the same breeding population that wintered apart (Rolshausen et al. 2010).

Here, we studied the association between morphology and migratory behaviour in a Blackcap population from Eastern Spain, in which individuals belong to one of the following three migration categories: all-year resident local birds (R), local breeders that migrate in winter (M) and northern breeders that winter in the area (W). First, we tested if local breeders are morphologically similar to northern Spanish migrants by applying the discriminant function of de la Hera and colleagues (2007) to our data. In a second step, we tested through season-specific discriminant functions if all-year residents (R) were morphologically different from northern migrants (W) and from local breeders that migrate in winter (M). Finally, we tested if R and M birds were distinguishable by their isotopic signatures (δD) in claws or tail feathers.

2. Methods

The study site was located along the riverbank of the river Serpis valley, in the municipality of Cocentaina (38° 44' N - 0° 44' W Alicante, Spain). The landscape of the area is a hilly and Mediterranean environment located between 400 and 500 m a.s.l. Annual precipitation is about 260 mm/year, and average temperature 13.4°C. The area is widely covered with olive groves and characterised by scarce broadleaf vegetation mainly concentrated on the bottom of the valley. Field work was performed during three breeding seasons (2010, 2011 and 2012), and two wintering seasons (2010-2011 and 2011-2012). We considered as breeding season the period between the 20th of March and 15th of August, and as wintering season the period between the 20th of November and the 25th of February. Blackcaps were captured with standard mist-nets, sometimes with help of tape lure to increase capture probability. Immediately after capture, morphological measurements were taken, all by the same person (MM), following standard ringing methods (Svensson 1992). All morphological characters were measured to the nearest 0.5 mm. We measured tail length, maximum wing chord length and right tarsus length. We also recorded the distances from the tips of primary 1 and 9 to the wing tip (hereafter primary distances PD1 and PD9, respectively), measured with the wing folded. Given that the difference PD1-PD9 increases as the wing becomes more pointed (Lo Valvo et al. 1988, Mönkkönen 1995), we considered it as an index of wing pointedness. Blackcaps were sexed and aged according to plumage characteristics (Jenny and Winkler 1994). In total we captured and measured 873 Blackcaps during the five field seasons.

2.1 Bird classification based on individual capture-recapture histories

Our Blackcaps were classified as "northern migrants" (W), "all-year residents" (R) or "local migrants" (M) based on individual capture-recapture histories. Individuals that were captured in the two winter seasons but never in spring or summer were classified as W. The origin of these birds is assumed to be central and northern Europe, as recapture maps for Spain suggest (SEO/birdlife 2012b). In addition, we have direct evidence for a northern origin of these birs by recapturing one individual ringed in Belgium and another in Germany. R and M birds constitute the local breeders in our study area, being the R the ones observed in the area, at least, in one winter plus one breeding season, while M birds were the ones captured in, at least, two breeding seasons but never during a winter season. This latter fraction of the population (M) is supposed to leave the area in winter. Both M and W birds are classified assuming that "non-recapture events" correspond to a real absence of the birds in the study area. Using this criterion, we classified a total of 70 birds: 27 W, 28 R and 15 M. Measurements of 3 of these birds (2 R and 1 W), for which we could not determine the age, were included only in those analy-

ses in which adults and juveniles were pooled together.

2.2 Comparison of the morphology with other Iberian populations

We applied the discriminant function by de la Hera et al. (2007), which originally aimed at discriminating migratory Blackcaps captured in central and northern Spain (Álava and Madrid) from sedentary ones captured in southern Spain (Gibraltar area), to test whether the morphology of Blackcaps in Cocentaina show the characteristics of migratory populations. The ultimate aims of this test were (1) to test the generality of the effectiveness of the morphological function calculated in an extreme-southern area, and (2) to detect inconsistencies between migratory behaviour inferred from capture-recapture histories and from flight morphology.

2.3 Discriminant function analysis

To perform discriminant function analyses (hereafter DFA), we selected morphological traits that have previously been shown to be suitable for identifying conspecifics with different migratory strategies both in Blackcaps and in other bird species (Pérez-Tris et al. 1999, de la Hera et al. 2007, Fudickar and Partecke 2013, Jahn et al. 2010a). Selected morphological traits were: (1) Tail/wing ratio, (2) wing pointedness (PD1-PD9), (3) length of the 8th primary feather (P8), and (4) tarsus length. Measurements of the four morphological traits were normally distributed among all the subsets and no outliers were found. We computed two sets of discriminant functions (Huberty and Olejnik 2006): one for the winter period, which aimed at discerning between R and W birds and a second for the reproductive season, which instead aimed at discerning between R and M birds. In the DFAs, the *a priori* probability of belonging to a migratory type was set proportional to sample size. Before we run DFAs, we checked by the means of ANOVAs if morphological traits significantly differed between sex or ages classes. If we detected significant differences, we performed additional specific DFAs for each sex and/or age subgroup. Thereafter, we checked the explanatory power of each DFA by looking at the proportion of correctly classified individuals. In addition, we performed a logistic regression with status of the individual (respectively R/W for winter and R/M for spring) as dependent variable and as covariates the same four morphological traits considered in the DFAs, as well as sex and age as factors. By progressively removing the non-significant explanatory variables, we determined which factors were significantly related to the birds migration status. Analyses were carried out with IBM SPSS 13.0 software.

2.5 Stable isotope analyses

With the aim of discerning between fractions of the breeding populations that wintered in different areas, we analyzed claw tips and feathers (second-last external tail feathers) collected in early spring as sampling tissues. Claws constitute a reliable source of dietary and habitat isotope signatures and their growth rates provide evidence that the information is integrated over a medium time scale such as weeks to months (Bearhop et al. 2003). Hence, claw tips of

birds captured just after arrival in spring appropriately reflect the isotopic signature of their wintering grounds (Bearhop et al. 2005; Rolshausen et al. 2010). Blackcaps grow their tail feathers in the breeding areas. This holds true for both adults, which renew them during the post-reproductive annual complete moult at the end of the summer, and juveniles, in which plumage start to grow in the nest before fledging (Shirihai et al. 2001). Thus, tail feathers reflect the isotopic signature of the birds' breeding grounds (de la Hera et al. 2012). Overall, we expected that M and R birds should differ for deuterium proportion in claws but not in feathers, and in particular individual differences between claw and feather signature should be higher in M than in R. Samples were collected in early spring 2011, between 29 March 2011 and 27 April 2011, and a majority of the feathers were sampled between 29 March and 1 April. Both claws and feathers were cleaned in 2:1 chloroform:methanol solvent rinse and prepared for stable hydrogen isotope analysis at the Agroisolab of Jülich, Germany. Measurements of $^{2}H/^{1}H$ are expressed in the typical delta notation (δD), in units per mil (‰). Because isotopic analyses are costly, we choose to analyse samples of birds that had previously been classified as M/R by recapture histories (see above) and then a further sample of 31 blackcaps of unknown migratory behaviour, with the aim to classify these birds as M or R based on the differences emerged from the samples of individuals of known migratory behaviour. As control of the claw δD values, we also sampled tips of the claws from some birds belonging to species of known migratory behaviour (i.e. residents or trans-Saharan migrants). This control sample was composed by 2 *Luscinia megarhynchos* and 1 *Hippolais polyglotta* belonging to the group of trans-Saharan species, and 3 *Cettia cetti* and 3 *Sylvia melanocephala* as resident species. Similarly, as control sample for feathers, we used δD signature of tail feathers from two blackcaps recaptured in Cocentaina, but ringed in northern Europe (one from Germany and other from Belgium). Differences in δD signature between different categories of birds were explored using ANOVAs.

3. Results

3.1 Migratory or resident shaped?

Out of 873 Blackcaps that we captured during the 5 seasons and for which all required measurements were available, 862 (98.74%) were classified as "migratory shaped" by the discriminant function given by de la Hera and colleagues (2007). Therefore, they were morphologically more similar to migratory Blackcaps from central northern Spain than to the resident ones from Gibraltar areas. This sample of 862 "migratory shaped" Blackcaps included all the 70 birds that we were able to classify as W(27)/M(15)/R(28) by their individual capture-recapture histories. In other words, behavioural differences assessed in the field were not reflected in mor-

phology, relying on the discriminant function of de la Hera et al. (2007). We cannot draw any firm conclusions on the 11 birds that were classified as "sedentary shaped" with this discriminant function, because none of these were classified following our M/W/R classification, given that they were captured only once.

3.2 Winter classification (W vs R)

We explored possible sex and age differences in the measurement of the morphological traits considered in the DFA, which overall yielded no significant results (all p>0.05). However, females had notably shorter eighth primary (P8) than males both in R and W birds (ANOVA R birds: $F_{1,26}$ =3.796; p=0.062; W birds: $F_{1,25}$ =11.721; p=0.060). Although differences were not statistically significant at p=0.05, we considered that was more conservative to perform further discriminant analysis taking into account sex. Equations of the final functions and significance values of Wilk's λ are given in Table 1. The Discriminant Function (DF) calculated for the whole winter sample was highly significant (p=0.002), and correctly classified 67.30% of the birds [19 out of 27 R and 16 out of 25 W]. The same function correctly classified 73.5% of the males [13 out of 19 R and 12 out of 15 W], and 55.56% of the females [6 out of 8 R and 4 out of 10 W]. Sex-specific discriminant functions had better values of Wilk's λ (males: 0.629 and females: 0.505), and were significant in both cases (p=0.002 and p=0.049 for males and females, respectively). The functions for males correctly classified 79.41% of the individuals [16 out of 19 R and 11 out of 15 W], while the functions for females correctly classified 83.33% of the individuals [7 out of 8 R and 8 out of 10 W]. The final logistic regression with R/W as dependent and morphological traits as predictors only retained tail/wing ratio in the model (β ± s.e. = 46.75 ± 13.75, p=0.001; Figure 1). According to our results tail/wing ratio is by far the most important discriminant factor between R and W

Table 1

Results of morphological discriminant function on flight-related traits aimed to discern local residents (R) from northern migrants (W), and the resident (R) from the migratory (M) fraction of the locally breeding partially migratory Blackcap population. Significance of the discriminant function is given by Wilk's λ test. Three functions were calculated for the winter cohort, one for the full sample and another for each sex. No function calculates given for the spring cohort, since p > 005. Columns give traits (see text for details) and coefficient for each trait considered in the final equation.

Season	Sample	Wilk's λ	p	R/W	intercept	Tarsus	Tail/wing	P8	PD1-PD9
Winter (W/R)	full	0.698	0.002	R	-1506.166	29.802	1804.023	13.894	13.954
				W	-1472.431	29.445	1753.013	14.229	13.598
	males	0.629	0.002	R	-1914.588	32.297	2162.172	21.489	18.260
				W	-1886.964	30.997	2116.889	22.114	18.285
	females	0.505	0.049	R	-1028.227	19.116	1230.132	10.291	8.252
				W	-1004.100	19.699	1156.654	10.970	6.984
Spring (R/M)	full	0.895	0.376	-	-	-	-	-	-

birds. In the DFA, tail-wing ratio resulted in coefficients two order of magnitude higher than other factors, while in the backward logistic regression this was the only explanatory variable retained.

3.3 Spring classification (R vs M)

None of the considered morphological traits differed between sexes or age in the breeding cohort [ANOVAs: F≤3.796 and p>0.062 in all the cases], so group-specific DFAs were not needed in this case. The discriminant function aimed at discerning by morphology between the migratory (M) and resident (R) fraction of the partially migratory population, but it was statistically non-significant [λ = 0.895, p=0.376]. Logistic regression gave similar results, because the morphological variables, as well as the categorical predictors of sex and age, were progressively excluded from the model (all p>0.05).

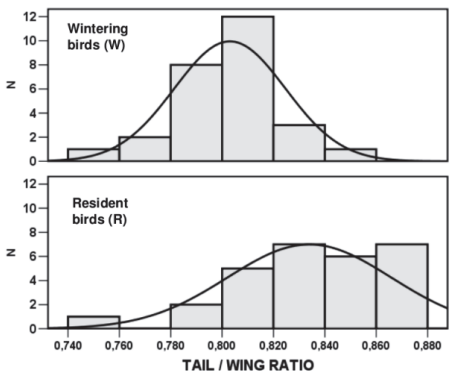


Figure 1
Distribution of tail/wing ratio between local resident (R) and northern migrant Blackcaps (W).

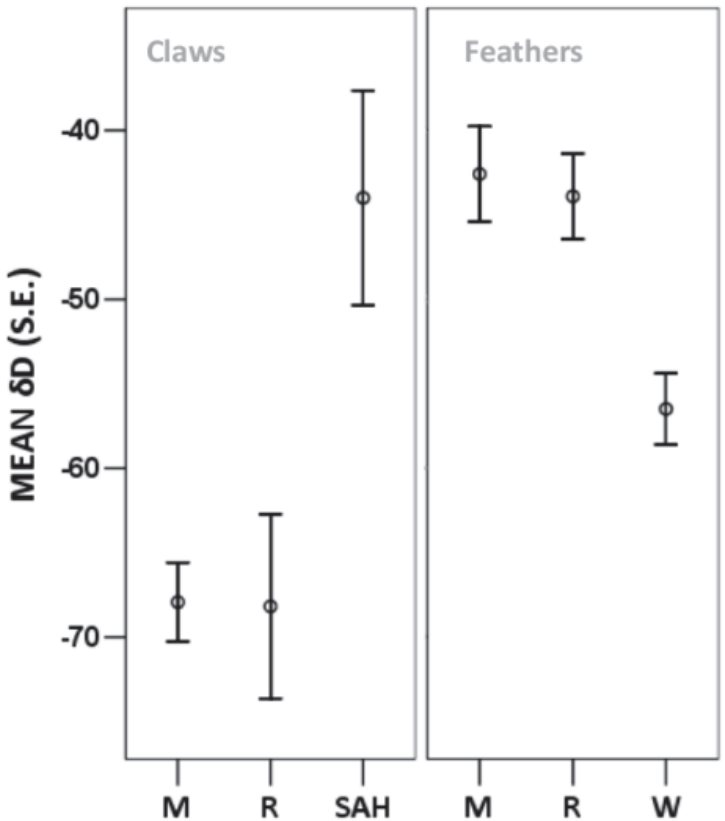
3.4 Isotopic signatures

δD signatures in claws of trans-Saharan migrants were clearly different from the three categories of blackcaps ($F_{2,16}$=5.290, p=0.017; Figure 2). However, if δD signatures in claws of blackcaps classified as M were directly tested against the value of samples from R birds, no significant difference emerged ($F_{1,14}$=0.002, p=0.967, see Figure 2). Similar results were obtained for the feather samples, given that the δD signatures in feathers of the two northern Blackcap samples clustered apart with a significantly lower δD ($F_{1,19}$=4.900, p=0.039; Figure 2), but M and R did not differ for this parameter ($F_{1,17}$=0.111, p=0.743). According to this finding neither the δD signatures of feathers nor claws of blackcaps of unknown migratory behaviour segregated in two different groups. Only one single individual (possibly a late migrant caught when passing through the area) showed extreme isotope signatures in claws and feathers, with values similar to those found in trans-Saharan migrants (Figure 3). Indeed, lack of difference in the feather's δD signatures of M and R birds was expected because these feathers reflect the isotopic signature of the breeding grounds and M and R birds are expected to breed sympatrically. Similarly, the lack of segregation in different groups of this value in the cohort of birds of unknown behaviour should at least confirm that they all are local breeders from the same population. However, we tested the feathers' δD signature with the principal aim to test whether individual differences between claw and feather values were clustering apart in M and R birds and to use even-

tual differences as a way to classify in M or R from the group of Blackcaps of unknown migratory behaviour for which we had analogous data (see methods). The results of this comparison show that the distribution of individual differences between claw and feathers signatures statistically differs between M birds and the group of birds of unknown migratory behaviour ($F_{1,35}$=5.303, p=0.027). However, the direct comparison between R and M was not possible because we had both claws and feather δD values only for two R birds, and the values strongly differed between them (see Figure 4).

Figure 2

Comparison of isotopic signature (proportion of deuterium, δD) in feathers and claws as compared between the two fractions of the partially migratory breeding population: all-year resident (R) and migrants (M). As control samples, claws from trans-Saharan species (SAH) and feathers of northern Blackcaps wintering in the area (W) were used. In general, it is considered that lower values of δD progressively correspond to more humid areas.. No differences between M and R value were detected.



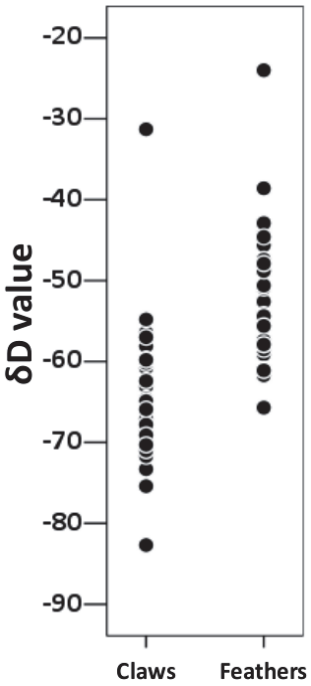


Figure 3
Distribution of isotopic signature (proportion of deuterium, δD) in claws and feathers of 31 breeding Blackcaps with unknown migratory behaviour. Neither feather nor claw values segregate in two clusters, as expected to disclose a partially migratory condition of the population.

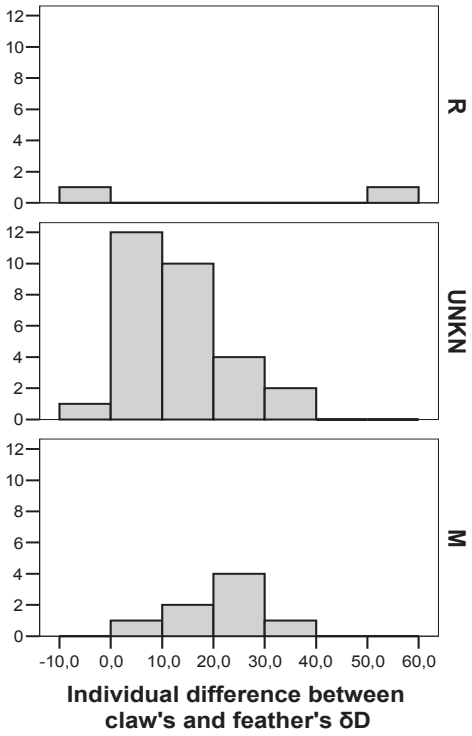


Figure 4
Distribution of individual differences between δD in claws and feathers of Blackcaps captured at Cocentaina and classified as M and R according to their recapture histories and others 31 local breeders of unknown behaviour. Even if M values appear to be higher than the mean of the unknown sample, the comparison between R and M is hampered because of the very small sample size for R birds.

4. Discussion

Individual capture-recapture histories demonstrate that some individuals from the local breeding population of Blackcaps behave as resident birds, being captured both during spring-summer and winter. This finding is the first demonstration of the presence of sedentary Blackcaps in this area of the Iberian Peninsula. Studies carried out in adjacent areas did not identify resident Blackcaps (Leal et al. 2004, Belda et al. 2007). This was probably due to the fact that individuals were captured in orange groves, a suitable environment for Blackcaps to overwinter but not for breeding (Gil-Delgado 1983).

Resident Blackcaps, as well as almost all the other birds from our study site, were classified as "migratory shaped" by the discriminant function defined by de la Hera et al. (2007). This incoherence with recapture histories indicates that discriminant functions based on flight morphology are not of general validity and need to be estimated using site-specific data. More interestingly, our result suggests that the general morphology of the studied Blackcaps from Cocentaina is more similar to the migratory Blackcaps of central and northern Spain than to the sedentary population from the Gibraltar area. This morphological similarity supports the hypothesis that the breeding population of Cocentaina originates from fully-migratory populations of northern-central Spain, as occurred in many other Blackcap populations at least in south-western Europe (Pérez-Tris et al. 2004). Thus, residency in Blackcaps from Cocentaina would be a derived character, which was only acquired in recent times. Therefore, it is likely that natural selection is favouring the emergence of a "sedentary shape" in flight morphology of this population, but the elapsed time since the acquisition of residency is too short to observe the phenotypic response to this selection. Blackcap populations can evolve sedentary behaviour in only a few generations (Pulido and Berthold 2010), and this time lapse is possibly too short to quantify the effect of selection on morphology traits. Exceptional circumstances, as strong reproductive isolation possibly achieved by assortative mating, may accelerate the occurrence of evolutionary changes that substantially affect morphology. Under these conditions morphological divergences may emerge in less than 30 generations (Bearhop et al. 2005, Rolshausen et al. 2009). However, strong reproductive isolation between the two fractions of our study population are not expected. In this population sedentariness or migratoriness of individuals is probably largely ecologically determined (i.e. birds migrate only in extreme harsh winters), as happen in general in partially migratory populations (Pulido 2011). Such state-dependent selection hampers any option to shape flight morphology toward a sedentary phenotype. A detailed mapping of the association of migratory behaviour and morphology in populations of Blackcaps in the central and oriental Iberian Peninsula, may identify other similar cases of incoherence between morphology and behaviour, and would shed light on the timing and the

causes of the loss of migratory behaviour.

Climate warming may be claimed as one of the factors involved in this "sedentarisation" (Pulido and Berthold 2010), but in our study population land-use changes are more likely to have had a key role in facilitating this process. For example, the increase in productivity of the olive groves gained by the improvement of the agricultural techniques possibly increased the availability of food resources for Blackcaps during winter (Rey 1993).

Despite the "migratory morphology" shown by breeding birds from Cocentaina, they still differ morphologically from migratory Blackcaps from central and northern European wintering in the area. Local birds have longer tails and shorter wings compared to northern conspecifics. This is pattern is similar to the pattern found in other studies which compare for sedentary with migratory populations in species other than the Blackcap (Leisler and Winkler 2003, Fiedler 2005, Neto et al. 2013). Discriminant power of the functions that we calculated (around 80% of the birds were correctly classified), however, is lower than in the similar studies conducted in the Gibraltar area where the rate of correctly assigned birds exceeded 90% (Peréz-Tris et al. 1999). Our results show that the morphological differences between residents and northern migrants found in the Gibraltar region, can be observed in other Iberian Blackcap populations. However, our results also suggest that this discrimination apparently progressively loses power when considering more northern populations. Overall, this suggests that despite of their real behaviour, morphological features of Iberian Blackcaps vary along a cline (e.g. Mullen and Hoekstra 2008), having a more migratory appearance in the north.

Deuterium signature (δD) in claws of trans-Saharan migrants clearly differed from signatures in all other birds ($F_{2,16}$=5.290, p=0.017; Figure 2). This results demonstrate the effectiveness of the isotopic signature in claws to locate the wintering sites of birds, at least to discern long from short-distance migrants. δD signatures in feathers of resident and migratory birds also differed, and it was a useful tool to discern between both categories (de la Hera et al. 2012). However, stable isotopes analysis completely failed in discriminating between migrants and residents of the local breeding population. We expected to find a bi-modal distribution of δD values in claws, which would represent the signature of the different wintering areas (Bearhop et al. 2005; Rolshausen et al. 2010). This distribution should have (1) reflected the classification of birds by recapture histories in M and R, (2) have allowed us to assign a range of unequivocal δD values to each category, and (3) have provided us with a tool to a posteriori classification of the migratory status of birds from this population. None of these expectations was fulfilled, so we conclude that M and R birds cannot be discerned by their isotopic profiles. The morphological approach lead us to the same conclusion, since it did not give any indication of differences between the breeding birds classified as M or R. In conclusion, we found no association between morphology or isotopic profiles with the partially-migratory

pattern deduced by capture-recapture histories. The most interesting result emerging from the isotope analysis was that the individual differences between claws and feather values is suggested to be a useful parameter to discern between migratory and resident individuals from a partially migratory population (Figure 4). However, the lack of a sufficient R sample prevented us from taking a definitive conclusion about this difference, but we believe that future explorations may be fruitful to confirm the pattern observed in other species.

Our methods for classifying the migratory status of a bird (M/R/W) possibly overestimated the migratory fraction of our study population of Blackcaps, given that a bird that is not recaptured in winter is considered as absent from the site. Capture effort in the study area was large during all the seasons, and therefore we assume that this overestimation had little influence on determining the migratory status by capture-recapture histories. At the same time, theoretical models on the control of partial-migration offer a good explication for the lack of morphologic and isotopic differences within a partially migratory population. These models predict that (1) migrants from this population migrate over short distances, and (2) that the migratory character in these populations is largely state-dependent, and not rigidly genetically determined (Pulido et al. 1996, Pulido 2007b and 2011). Both of these predictions have been recently demonstrated in a partially migratory population of Eurasian blackbirds (*Turdus merula*), in which migrants spend the winter close (40-300 Km) to the breeding sites and migration is a state-dependent condition, in which only females migrate (Fudickar and Partecke 2012, Fudickar et al. 2013). Given the short migration distances, changes in δD proportions between migrants and residents could not be detected (Fudickar et al. 2013). This is also expected in our study, because distance between the breeding and the putative wintering areas located in Southern Iberian Peninsula or northern Morocco is too small to detect different wintering sites, especially given that in the Iberian peninsula the latitudinal cline in δD is very shallow i(Figure 1 in Bearhop et al. 2005). In a previous study, Blackcaps wintering in two different areas have been identified using δD profiles in claws (Bearhop et al. 2005, Rolshausen et al. 2010), but the wintering sites (i.e. southern Europe and England) were separated by more than 2000 km and 10 degrees of latitude.

As for isotopic profiles, morphology may be similar between migrants and residents in partially migratory populations. For example, in the Blackbird populations mentioned above (Fudickar and Partecke 2012, Fudickar et al. 2013), no differences in wing and tail length were found between migrants and residents, whose migratory status was reliably determined by tracking individuals using aerial radio-telemetry (Fudickar and Partecke 2012). This was interpreted as a consequence of state-dependent migratory behaviour because females are obligate migrants, while males behave as residents (Fudickar et al. 2013). Thus, if partial migration is a state-dependent condition that may change during the life of an individual (e.g. because of the gain of experience or because of yearly

oscillation in environmental conditions), no morphological differences are expected to evolve between groups of individuals within a population. Overall, the lack of morphological differences between the two fractions of our partially migratory population suggests that in this population migratory behaviour is a state-dependent condition, which, as a consequence, sets aside the possibility for morphological divergence by natural selection. This suggestion is reinforced by the fact that Blackcap populations are known to have the potential for rapid evolutionary changes, both in migratory behaviour (Pulido and Berthold 2010, Berthold et al. 1992) and morphological traits (Rolshausen et al. 2009), but that strong genetic isolation is a condition which must be met for this to occur.

In conclusion, our results give new insights on the relationship between morphology and migratory behaviour, showing that Blackcap populations of "migratory" appearance can behave as residents. This fact suggests that flight morphology evolves at a slower rate than migratory behaviour. Moreover, our results confirm that the association between migratory behaviour and flight morphology, which has been found both intra- and interspecifically, and is disrupted in partially migratory population. In these populations the morphologies of resident and migratory individuals largely overlap.

The results presented here call for an in-depth exploration of the ecological factors that determine the migratory status of individuals within a population. For example, it is possible that birds of different sex or age categories have different abilities to compete with conspecifics that overwinter in the same geographical area (e.g. Pérez-Tris and Tellería 2002), which will result in different pressures to migrate. The knowledge of the control of migratory behaviour in natural bird populations is still scarce and thus, it is difficult to predict how the adaptive morphology associated with a migratory phenotype co-evolves with changes in migratory behaviour itself. Clearly, partially migratory populations and populations of birds that are currently undergoing changes in their migration habits are the best systems to obtain the information needed to answer this question.

CHAPTER VII

Dominance and habitat selection in sympatrically wintering Blackcaps (*Sylvia atricapilla*)

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Unpublished manuscript.

Abstract

Birds show a wide variety of migratory patterns within and among species. Maintenance of this variation strongly depends on conditions during the wintering seasons, particularly in resident populations, which in winter share their breeding sites with migratory conspecifics. Dominance and spatial segregation have been suggested as the main mechanisms facilitating this coexistence. This, however, has been supported so far only by indirect evidence.

We directly tested this hypothesis by determining the effects of intrinsic factors (e.g. sex, age, body size, body conditions and migratory behaviour) on social ranking, habitat use and size, and habitat composition of the home ranges in migratory (W) and resident (R) blackcaps (*Sylvia atricapilla*) wintering in the same area. Direct observations of aggressive interactions between individually-marked birds were used to assign individual dominance scores. Home ranges size, composition and selection of winter habitat were determined by radio-telemetry during two consecutive winters.

The mean ratio of migratory to resident birds was 2.5:1, but strongly varied between age and sex classes, resident females being almost absent. Resident birds were dominant over migratory birds, although on average they were smaller in structural body size. Compared to resident birds, home ranges of migratory birds was of the same size, but had higher habitat diversity. Resident and migratory birds did not differ in habitat use.

Our results shed light on the mechanisms that maintain migratory and sedentary behaviour in wild bird populations. These mechanisms may also explain the occurrence of partial-migration in the local breeding population. Overall, our findings support the hypothesis that the interactions among migratory and resident birds in wintering quarters explain the maintenance of large variation in migratory behaviour, as observed in the Blackcap at the intra-specific level.

1. Introduction

Migratory birds profit from the high productivity of seasonal environments during some periods of the year. This enables migratory species to live in ecological niches that are only available for a short period of the year cycle, and to avoid harsh winter conditions in their breeding quarters (Alerstam et al. 2003). However, migration has costs in terms of time and energy invested in migratory movements and of higher predation risk and parasitism, which are the cause of high mortality (Newton 2008, Klaassen et al. 2014). It is hypothesized that trade-offs between costs and benefits of migration maintain large variation in migratory strategies. While billions of birds travel thousands of kilometres between breeding and wintering quarters every year (Hahn et al. 2009), in milder, less seasonal climates, sedentariness may be the most adaptive strategy, given that the costs of remaining on the same territory during the whole year may be reduced. This may be the ultimate cause for the latitudinal cline in the proportion of migratory species (e.g. Newton and Dale 1996 a,b). Latitudinal clines in the tendency to migrate are also found within species, whereby the frequency of migratory individuals increases towards the poles. At temperate middle latitudes, the migratory status of a population is not easy to predict. Selective factors favouring migration may be relaxed in milder climates, often leading to the evolution of partial migration. This is the situation in which one part of the population migrates while the other part is resident (Chapman et al. 2011). In this sense, two types of partial migration are recognised: (i) *non-breeding partial migration*, in which migrants and residents breed together but winter apart (e.g. Blue tit *Cyanistes caeruleous*, Nilsson et al. 2010), and (ii) *breeding partial migration*, in which migrants and residents overwinter together but breed allopatrically (e.g. American Dipper, *Cinclus mexicanus*, Gillis et al. 2008).

The Blackcap (*Sylvia atricapilla*) is a widespread common bird of the western Palearctic that shows populations of all possible migratory strategies, from completely resident to long-distance migratory (Shirihai et al. 2001). Populations from coastal southern Europe are resident or non-breeding partial migrants that in winter share their breeding areas with migratory conspecifics that breed in northern European. Thus, in coastal areas of eastern Spain, where we conducted our study, three Blackcaps populations differing in migratory behaviour are present throughout the annual cycle. This situation had been previously described for blackcap population in southern France (Berthold 1986).

In Iberia, Blackcaps are generally completely resident in the south and in coastal areas (e.g. Gibraltar area), while populations from the interior and north are completely migratory (Tellería and Carbonell 1999, Shirihai et al. 2001, Pérez-Tris et al. 2004). Every year, large numbers of Blackcaps breeding in northern and central Europe spend the

winter in Iberia (Cantos 1995). Given this situation, previous studies aimed at knowing how resident individuals cope with competition with northern migrants to ultimately understand how resident populations can persist (Pérez-Tris and Tellería 2002, de la Hera et al. 2012, Tellería et al 2013). These studies identified habitat segregation between migrants and residents as an important mechanism to reduce competition. Resident individuals were only distributed in forest patches (where more varied and abundant food can be found), while most of the wintering individuals were confined to shrublands (Pérez-Tris and Tellería 2002, de la Hera et al. 2012). This distribution, coupled with the fact that resident birds are usually larger than migrants, suggested that body size-mediated dominance is the mechanism that maintains spatial segregation in a blackcap population from Gibraltar (Pérez-Tris and Tellería 2002).

Certainly, the issue of spatial segregation needs further study. General questions emerge from the fact that residents maintain the same territory throughout the year (e.g. Adriaensen and Dhondt 1990, Pérez-Tris and Tellería 2002), but different categories of individuals may differ in their ability as well as in their need of maintaining it. Therefore, we needed to explore which individuals of the breeding population behave as resident, and how the populations of both year-round residents and wintering birds are composed. A specific question to be addressed is whether spatial segregation entails differences in resource use. Previously, it was found that resident and wintering Blackcaps, which used different habitats, did not differ in their diet (Tellería et al. 2013). In the present work, we approach the question of spatial segregation and habitat use by studying home ranges of individual Blackcaps using radio telemetry throughout the winter. Specifically, we tested whether sex, age, body size, body conditions or migratory behaviour (resident vs northern migrant) had an effect on home range size and composition, and habitat use.

Dominance relationships are one of the main factors determining habitat segregation in winter and migratory behaviour in (non-breeding) partially migratory populations (e.g. Gautheraux 1978, Lundberg 1985, Berthold 1986, Adriaensen and Dhondt 1990, Bai 2012). As a rule, subordinate individuals (i.e. juveniles and females) are more prone to be driven to suboptimal winter habitats (Marra 2000) or to migrate (Gautheraux 1978, Ketterson and van Nolan 1988). Dominant individuals of the local breeding population may behave as residents because they can compete with migrants wintering in the area (see Berthold 1986). Thus, studying the variables that determine winter dominance will also shed light on the ultimate factors that maintain partial migration in the local breeding populations.

Overall, the above-mentioned studies call for empirical field evidence demonstrating that competitive interactions between resident and migrants actually occur in their sympatric wintering grounds and identifying the factors that determine their outcome. Here, we present first insights into these questions using observations of individually

marked birds, previously classified as wintering or resident by a morphological discriminant function (see Chapter VI).

2. Methods

2.1 Study area

Field work was conducted along the River Serpis valley, in the municipality of Cocentaina (38° 44' N - 0° 44' W, Alicante, Spain). Landscape is a hilly and Mediterranean environment (400-500 m a.s.l.), dominated by olive groves. Broadleaf vegetation is scarce and mainly concentrated on the bottom of the valley. Climate is semi-arid Mediterranean (annual rainfall: 263 mm/year, mean annual temperature: 13.4°C).

2.2 Field work and statistical analyses

Captures by mist-netting were conducted between the 20th of January and the 20th of February both in 2011 and 2012. Radio-tracking, ringing and observations were alternatively conducted from dawn to dusk following a scheme to homogeneously distribute each type of sampling during the whole daylight. Blackcaps were trapped using mist-nets and were individually marked with aluminium rings and a unique combination of colour rings to allow identification from a distance. All morphological measurements were taken by the same observer (MM), following standard ringing protocols (Svensson 1992). Maximum wing chord, wing pointedness and tail length were measured with a ruler with 0.05 precision. Right tarsus and length of beak were measured with an electronic calliper with 0.01 mm precision. Wing pointedness was calculated from the difference between the distances from the tips of primary feathers 1 and 9 (numbered in decreasing order, Jenny and Winkler 1994) to the wing tip. This measure is positively correlated with the pointedness of the wing (Pérez-Tris et al. 1999). Birds were classified as migratory or resident by the means of a discriminant function based on birds which migratory status was determined according to their individual recapture histories (details in Chapter VI). Differences in the proportion of wintering or resident individuals in different age ans sex classes was explored through generalized linear model with a Binomial distribution with a logit link function and sex and age as categorical predictors.

Furthermore, we calculated indices of body size and body condition of the birds, similarly to Pérez-Tris and Tellería (2002). To obtain an index of structural body size, we conducted a Principal Component Analysis (PCA) with the length of tarsus, beak, wing and tail. Components were varimax rotated. The first principal component (PC1) explained 40.75% of the variance and was positively correlated with the four variables (eigenvalue= 1.630; factor loading for tarsus length=0.384; beak length=0.259; wing length=0.883; tail length=0.798). We used this principal component as an index of structural body size. As a measure of individual fat accumulation, we used a fat score as-

signed by visual estimation of subcutaneous fat (Kaiser 1993). This variable was transformed by calculating the logarithm of the squared score to meet normality. Transformed fat scores were positively related to weight (Pearson correlation: r=0.599; p<0.001). We regressed weight on structural body size (β=0.466, p<0.001) and fat content (β=1.267, p<0.001) and used unstandardized residuals of this regression as an index of body condition. Body size and body condition indexes were unrelated (Pearson correlation: r=-0.013; p=0.773). The independence of these two variables suggests that the two indices represent different and unrelated sources of variation related to body size and body condition.

Before we used these indices as predictors in the models about dominance and home ranges, we explored their interactions with the other factors used as predictors in the models. With this aim, we performed linear models having as dependent body size or body condition index and as predictor age, sex and migratory behaviour (W/R) of the individuals.

2.3 Dominance analyses

Birds were classified according to their dominance using the ranking method originally proposed by Elo (1978) and successively adapted to animal systems, known as "Elo-rating" (Neumann et al. 2011). This ranking procedure has special advantages when compared to other classical methods of ranking [e.g. I&SI (de Vries 1998), and David's score (David 1987)], being especially suited for studying highly open systems, with a low number of interactions and in which the proportion of non-observed interactions is unknown, but probably high. Moreover, this method is independent of demographic changes and is independent of the total group composition, i.e. of the number of individuals present in the area when interactions occurs (Neumann et al. 2011). Elo-rating is a progressive method, so that individuals start all from a same score and progressively gain or lose points depending on the outcome of the interactions in which they are involved. The amount of scores won or lost in each interaction depends on the *a-priori* probability of the outcome of that interaction. A dominant individual, for instance, will gain progressively less points for each interaction won, while a "loser" that unexpectedly beats a "winner" will gain much more points (see Neumann et al. 2011 for further details). Thus, this approach considers the evolution of the relationships within a group and is a good way to assess the personality of individuals. We applied this method to analyse behavioural interactions observed on a group of kaki trees (*Diospyros kaki)* that were used as feeding place by Blackcaps in our study area in winter. We considered as aggressive interaction the observation of a bird actively chasing another. We only considered interactions in which both individuals were identified by colour rings (58 interactions involving 32 individuals). Analyses were carried out in R (R Development Core Team 2013), using the script provided by Neumann et al. 2011, with adjustment to read comma separated values (csv) files instead of Microsoft Excel (xls) ones (Cristof Neu-

mann pers. comm.) We maintained the default values of 1000 for the starting score and 200 for K (the parameter used to calculate the amount of points gain/loss in each interaction). "K" also reflects the probability that a winning individual will win the following encounter, which is two times the probability of winning for an individual that never won previous encounters (Rutte et al. 2006). We used General Linear Models (GLM, *nlme* package for R) to test if dominance was affected by sex, age (first-winter vs adults), migratory behaviour (W vs R), body size or body condition. We selected the best model by comparing AIC values among all the possible models built with any combination of the factors (31 + 1 null model). The choice of the parameter "K" (see above) is of minor importance over a large period, but may strongly affect ranking in a short series of matches (Neumann et al. 2011), as may be for our study case. We thus repeated the ranking procedure setting K to 500 and to 50 and test if best model selected on the three different ranking (K=200, 500 or 50 respectively) differed.

2.4 Factors determining home range size and habitat preferences

We followed winter movements of 30 Blackcaps in the study area (9 in 2011 and 21 in 2012). Radio-tracking was carried out by using small transmitters (0.42g, Pip41 tags by Biotrack), each tuned on an individual frequency. Transmitters were attached to birds by means of a rubber harnesses (see, Rappole and Tipton 1991). Sika receivers with range extension between 138 - 174 MHz and Yagi antennas with flexible element were used for tracking radio signals (for technical details, see www.biotrack.co.uk). Radio tags were attached to the birds in January. Birds were tracked untill the end of the wintering period (20th Feb), following a scheme, by which the position of each individual was determined at least once per hour, considering the time lapse from sunrise to sunset. All points obtained for each individual were finally merged into a unique home-range, which represents the area used throughout the winter. Home ranges were calculated with a mean (s.d.) of 37 (8.6) points for each Blackcap (range: 17-54).

Home ranges were calculated as fixed kernels at 95% using the "HRT tools" extension (Rodgers et al 2007) for ArcGis 9.3 (ESRI, Redlands, CA, USA). Smoothing parameter of the kernel (href) was individually-adjusted by selecting the smallest value of href (rounded to the nearest 0.05) for which the external boundary of the kernel remains continuous, following the progressive method described in the HRT tools manual (Rodgers et al. 2007). We tested if home range size was affected by sex, age, migratory behaviour, body size index, body condition index or year (2011 vs 2012) using a GLM. We selected the best model by comparing AIC values among all the possible models built with any combination of the factors (63 + 1 null model), excluding interactions between factors.

In order to explore distribution of birds in different habitats, we mapped the distribution of habitat types in the study area, starting from photointerpretation supported by a field confirmation of borders of the polygons and

pertinent habitat category. Mapping was performed in ESRI ArcGis 9.3 (ESRI, Redlands, CA, USA) and QGIS 1.7.4-Wroclaw (Quantum Gis Development Team). In the first phase, habitat types were defined following EUNIS categories, as defined by Davies et al. (2004) (but see also: http://eunis.eea.europa.eu/habitats.jsp) and adding new categories when habitat types present in the study area were not available in the EUNIS categorization. Overall, in this first step, we defined 20 habitat types (Table 1). Successively, we merged similar habitats in order to reduce the number of habitat types and improve the interpretative power of the model. We merged categories that were similar for vegetation macro-typology and management of olive groves (Table 1 for the habitat categories after merging). For testing whether the home ranges of contrasting different groups of individuals (males vs females; birds in their first-winter vs adults and residents vs migrants) showed different habitat composition, we derived a first series of dependent variables, obtained by measuring extension of each habitat type within each home range. This measure was used to express home range composition, or habitat availability. Habitat proportions were then log-ratio transformed previous to be entered in the model as dependent variables (Aebischer et al. 1993). In order to reduce Type I error, zero values were replaced with 0.005 (Bingham and Brennan 2004).

To explore habitat selection, we considered this at "third-order", as defined by Johnson (1980), which refers to the use of various habitat components within the home range of a single individual. This is a detailed view of resource use (Aebischer et al. 1993), exploring a deep and fine level of selection in which availability is represented by proportions of habitat categories inside home range, while use is defined by the relative proportions of habitat category in which telemetry locations fall inside the home range. We calculated the differences between the log-ratios for used and available habitats for each habitat category considered. This became the final dependent variables expressing habitat selection. We thus ran two MANOVAs in which we tested the effects of sex, age and migratory behaviour (W vs R). In the first MANOVA, dependent variables were those variables indicating habitat availability, while in the second one dependent variables were those indicating habitat selection. MANOVAs were run in the *car* package (Fox and Weisberg 2010) for (Venables and Smith 2010). Thus, the first model aimed at testing differences in the settlement of birds within the area, while the second model tested the effective use of resources during winter. In the models R, we also considered the potential effect of among-year differences in the availability of resources by including "year" as factor (2011 vs 2012). Non-significant factors were progressively removed from the model by stepwise backward procedure (Crawley 1993).

Table 1

Habitat typologies and relative EUNIS title considered in the habitat mapping.

	Macro-typology (final classification)	Habitat (first classification)	EUNIS code	EUNIS title
1	River and riparian vegetation	Running water	C2.2	Permanent non-tidal, fast, turbulent watercourses
		Riparian vegetation	C3	Littoral zone of inland surface water bodies
		Rubus sp. shrublands	F3.2	Submediterranean deciduous thickets and brushes
2	*Arundo donax* beds	*Arundo donax* beds	C3.32	*Arundo donax* beds
3	Sparsely wooded grasslands	Sparsely wooded grasslands	E7	Sparsely wooded grasslands
4	Open areas	Dry grasslands	E1	Dry grasslands
		Crops	I1.2	Mixed crops of market gardens and horticulture
		Bare soil	I1.5	Bare tilled, fallow or recently abandoned arable land
		Herbaceous communities of roadsides	J4.1	Disused road, rail and other constructed hard-surfaced
		Roads	J4.2	Road networks
5	Gardens and orchards	Almond plantation	-	no Eunis title available
		Orchards	FB.31	Shrub plantations for ornamental purposes or for fruit, other than vineyards.
		Gardens	I2.2	Small-scale ornamental and domestic garden areas
		Buildings	J2.1/J2.6	Scattered residential buildings/Disused rural constructions
6	Managed olive groves	Olive groves with absent or herbaceous underbrush	G2.91	*Olea europaea* groves
7	Not-managed olive groves	Olive groves with low shrub underbrush	G2.91	*Olea europaea* groves
8	Natural deciduous wood	Deciduous wood	G1.7C5/G2.12 /G1.3	*Celtis australis* woods / *Quercus ilex* woodland / Mediterranean riparian woodland
9	Poplar plantations	Poplar plantations with any degree of shrub underbush	G1.C1	Poplar plantations
10	Conifeorus forests	*Pinus halepensis* forests with any degree of underbrush	G3.741	Iberian *Pinus halepensis* forests
		Coniferous plantation	G5.4	Small coniferous anthropogenic woodlands

3. Results

3.1 Composition of the population in winter

A total of 493 Blackcaps were captured, of which 64.1% were classified as W, giving a ratio of 2.5 W for each R bird. Notably, the ratio W:R strongly differs among sexes and age classes (see Table 2). The model about the proportion of W/R birds showed that the proportion of resident birds was higher in males and juveniles [both p <<0.001, N=429 (birds of unknown age omitted)]. Among migrants, birds from the four sex-age categories (juvenile and adult males and females) were evenly distributed (Fisher's exact test, compared to even distribution: p=0.505). In the migrants, however, there was an excess of juveniles, which was close to significance (p=0.075, see Figure 1).

3.2 Body size and body condition

General linear models with body size or body condition index as dependent variables showed that adults are larger than juveniles (β±s.e = 0.477±0.10, p<0.001) and migrants larger than residents (β±s.e = 0.599±0.12, p<0.001). Sexes also differed in body size, but not in the same way in both populations: males were larger than in females among migrants, but smaller than females in the resident population [Sex: p=0.170; Sex*Wint/Res: β±s.e = -0.643±0.22, p=0.004. Figure 2]. This same result also shows that migrants and resident females had similar size, while migrant males were significantly bigger than resident ones. Model about body size has an overall high significance (p<<0.001), and an R^2 of 13.03. Body condition, however, did not significantly differ within any category of birds [Age: p=0.114; WR: p=0.814; Sex: p=0.845, Sex* Wint/Res: p=0.243, see figure 2].

Figure 1

Distribution of sex-age classes among all year resident (R) and northern European migratory (W) Blackcaps. Bars represent different categories of birds, from the left: adult males and females, first-year males and females, males and females of undetermined age. Total N = 493.

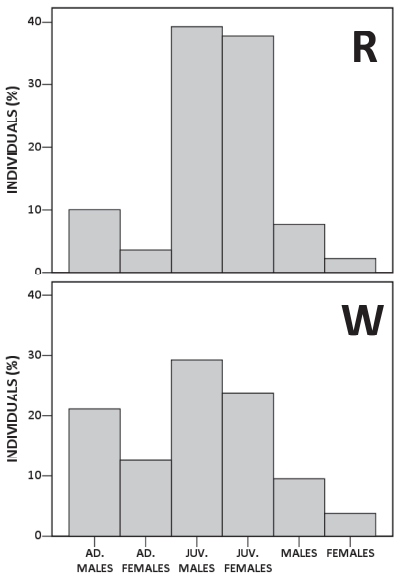


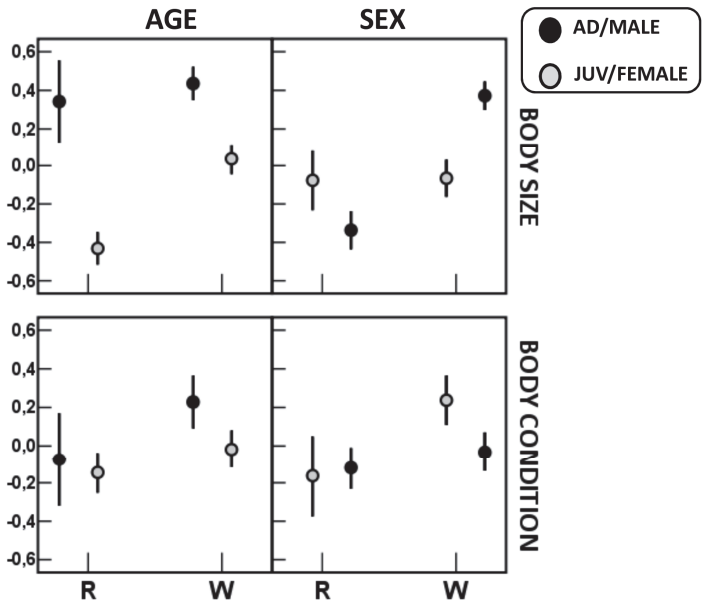
Table 2

Proportions of residents (R) and northern migrants (W) Blackcaps among different sex/age classes. Proportions were calculated relative to the birds present in the area in winters 2010-2011 and 2011-2012 after classification of birds based on the morphological discriminant function described in Chapter VI. Ratio W:R significantly differs between categories [χ^5_1 =30.613, p<0.001].

Sex	Age	N	W (%)	R (%)	Ratio W:R
Males	First-year	186	49.46	50.53	1:1
	Adult	90	73.33	26.67	3:1
	Unknown age	48	62.50	37.50	2:1
Females	First-year	105	71.43	28.57	3:1
	Adult	47	82.98	17.02	5:1
	Unknown age	17	70.59	29.41	3:1
Total sample		**493**	**63.69**	**36.30**	**2.5:1**

Figure 2

Mean (±S.E.) body size (upper line) and body condition index (lower line) in wintering Blackcaps differing in migratory behaviour (W or R), controlling for age (left column) and sex (right column). Black dots represent adults in age graphs and males in sex graphs. Grey dots represent first-year birds and females respectively. Sample sizes are the following: Male 330, Female 173; Juv (First-year) 285, Adult 152.



3.3 Dominance

Results of Elo-rating ranking of individuals are shown in Table 4.

Previous to model selection an outlier was eliminated from the database (an individual with dominance score near to 1600, see Table 4). The linear model testing the factors determining dominance score was then selected by the means of AIC values, and we obtained similar results despite the value of factor K used to calculate dominance scores (see 2.3 above and Table 3). In model selection, the same model ranked first in all the three series of rankings (Table 3). However, significance of the factors slightly varied depending on K (Table 5). Resident and larger birds have higher dominant scores, as reflected in the significance of the factor "migratory behaviour (W/R)" and near-significance of "body size" in all the cases (Table 5). Age and body condition were also retained in the best models, whereby birds with the lowest physical condition tended to have higher dominance scores. However, in no case any of these factors reached significance (Table 5). Simple relationships of body size, body conditions, age, sex and migratory behaviour with dominance score are shown in Figures 3 and 4.

Table 3

Best general linear models, predicting dominance score ordered by increasing Aikaike's Information Criterion (AIC). Models were considered equivalent when AIC difference (Δ AIC) was less than 2 units. Models deviating from the best model by Δ AIC > 2 are not shown. Sections within the table show models for different values of K (see Methods) WR= migratory or resident individual, BSIZE= body size index, BCOND= body condition index, AGE= first year vs adult, SEX=male vs female.

Rank	K value	Factors	AIC	ΔAIC
1	**200**	WR + BSIZE + BCOND + AGE	269.95	0.00
2	(default value)	WR + BSIZE + AGE	271.18	1.24
3		WR + BSIZE + BCOND + AGE + SEX	271.84	1.89
1	**50**	WR + BSIZE + BCOND + AGE	231.79	0.00
2		WR + BSIZE + AGE	231.84	0.05
3		WR + BSIZE + AGE + SEX	233.34	1.55
4		WR + BSIZE + BCOND + AGE + SEX	233.66	1.87
5		WR + BCOND + AGE	233.74	1.95
1	**500**	WR + BSIZE + BCOND + AGE	293.25	0.00
2		WR + BSIZE + AGE	294.42	1.17
3		WR + BSIZE + BCOND + AGE + SEX	295.15	1.90

Table 4

Dominance scores and individual characteristics of 32 Blackcaps observed in aggressive interaction with conspecifics. Dominance was calculated by the Elo-rating method setting K at the default value of 200 (Neumann et al. 2011). Birds are ranked from highest to lower score.

Rank	Dominance score	Sex	Age	Migratory Behaviour	Fat score	Body size index	Body condition index
1	1557	Male	Adult	W	2	0.208	-0.230
2	1275	Male	First-year	R	3	-1.629	-0.463
3	1233	Male	First-year	R	3	0.065	0.348
4	1211	Male	First-year	Undet.	4	-	-
5	1188	Male	Adult	R	2	0.597	0.769
6	1148	Male	Adult	R	2	-1.395	-0.684
7	1148	Female	Adult	W	3	0.298	-2.310
8	1148	Male	Adult	R	1	-0.716	1.031
9	1148	Male	Adult	W	2	0.819	-1.325
10	1072	Female	Adult	W	2	-	-
11	1056	Male	Undet.	R	3	0.718	-0.806
12	1000	Female	First-year	W	3	0.877	0.030
13	982	Male	Undet.	Undet.	2	-	-
14	978	Male	First-year	R	1	0.027	-0.265
15	968	Male	Undet.	Undet.	2	-	-
16	967	Female	Adult	R	2	-	-
17	966	Female	Undet.	Undet.	1	-	-
18	949	Male	First-year	R	1	-1.133	0.585
19	940	Female	Adult	W	2	-	-
20	921	Female	Adult	Undet.	3	-2.580	-0.700
21	919	Female	First-year	Undet.	3	-	-
22	906	Male	Adult	R	4	-1.278	0.821
23	869	Female	Adult	W	2	-1.123	1.510
24	852	Male	Undet.	W	4	0.000	1.126
25	852	Male	First-year	R	2	-1.179	-0.524
26	852	Male	Undet.	W	2	0.014	-0.300
27	852	Male	First-year	W	2	0.092	0.284
28	852	Male	Adult	R	4	-2.014	0.704
29	852	Male	First-year	W	6	-0.285	4.543
30	796	Female	Adult	W	2	-0.603	1.307
31	789	Female	First-year	W	2	-2.787	-0.226
32	754	Male	Undet.	W	0	0.048	-0.060

Table 5

Parameters in the best GLM of the variables affecting dominance score. Values are referred to models in which dominance score was calculated with different K value (see Methods). WR= migratory or resident individual, BSIZE= body size index, AGE= first year vs adult.

	Factor	β ± s.e.	p
K200	WR	141.35 ± 57.41	0.026
	BSIZE	55.02 ± 26.84	0.057
	BCOND	-35.23 ± 21.58	0.122
	AGE	36.19 ± 57.69	0.539
K50	WR	45.198 ± 23.14	0.069
	BSIZE	19.69 ± 10.82	0.088
	BCOND	-11.15 ± 8.70	0.218
	AGE	7.89 ± 23.26	0.739
K500	WR	266.02 ± 99.98	0.017
	BSIZE	100.01 ± 46.74	0.048
	BCOND	-60.67 ± 37.58	0.126
	AGE	74.74 ± 100.46	0.468

Figure 3

Relation between dominance score and indices of body size and body condition of 32 individually-marked Blackcaps observed in aggressive interactions. Resident (black dots) and migratory (grey dots) individuals are discerned.

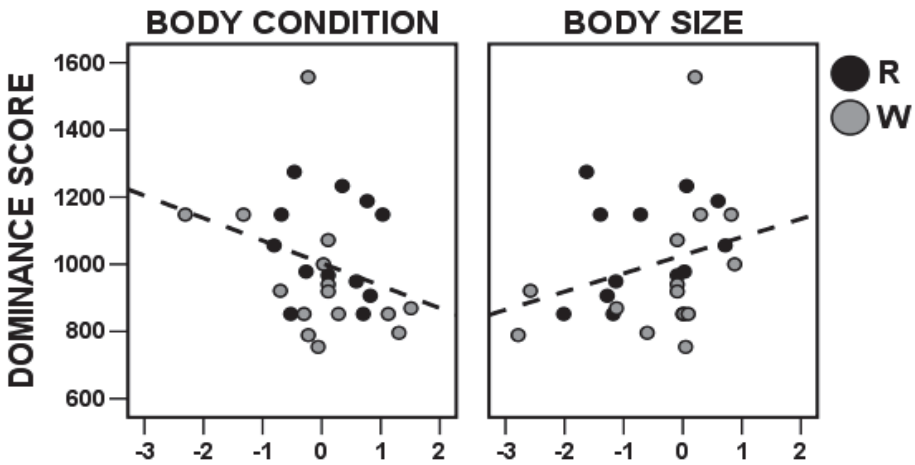


Figure 4

Mean dominance score in birds of different age (A), sex (B) and migratory behaviour (C). AD: adults, JUV: first-winter, MM: males, FF: females, R: resident, W: migratory. Sample sizes are given at the bottom of the boxes.

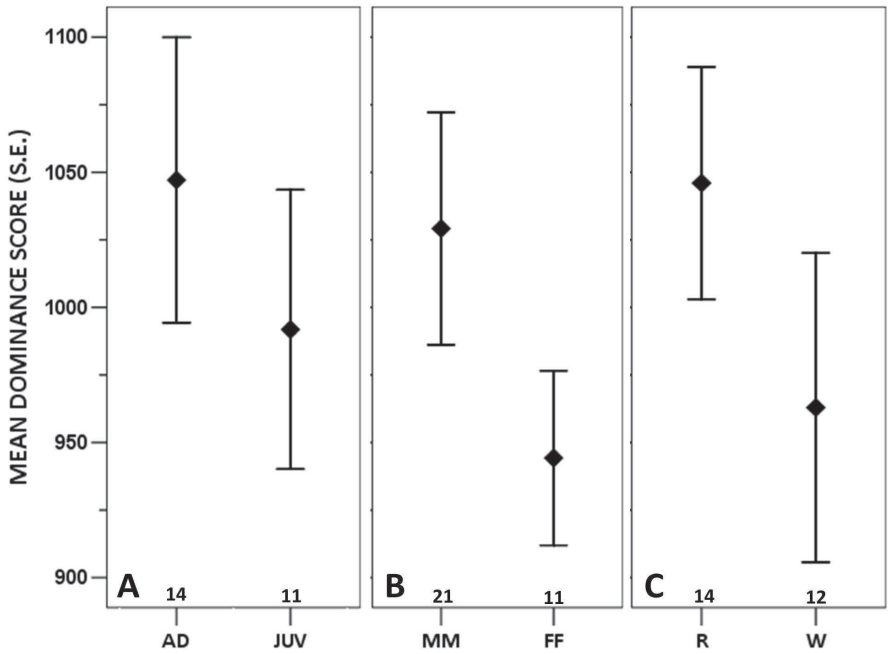


Table 6

Complete list of GLM explaining the factors affecting home range size, with respective AIC and ΔAIC values. WR= migratory or resident individual, BSIZE= body size index, BCOND= body condition index, AGE= first year vs adult, SEX=male vs female, YEAR= 2011 vs 2012.

Rank	Model	AIC	ΔAIC	Rank	Model	AIC	ΔAIC
1	WR	690.18	0.00	33	1(Null model)	735.40	45.22
2	WR +YEAR	691.50	1.31	34	AGE	736.70	46.51
3	WR +AGE	691.65	1.47	35	YEAR	736.90	46.72
4	WR +SEX	692.03	1.85	36	SEX	737.18	46.99
5	WR +BCOND	692.16	1.97	37	BCOND	737.38	47.20
6	WR +BSIZE	692.17	1.98	38	BSIZE	737.40	47.22
7	WR +SEX +YEAR	692.65	2.47	39	SEX +YEAR	737.97	47.78
8	WR +AGE +YEAR	693.26	3.07	40	AGE +SEX	738.36	48.17
9	WR +AGE +SEX	693.38	3.20	41	AGE +YEAR	738.43	48.25
10	WR +BSIZE +YEAR	693.48	3.29	42	BCOND +AGE	738.68	48.50
11	WR +BCOND +YEAR	693.48	3.30	43	BSIZE +AGE	738.69	48.51
12	WR +BSIZE +AGE	693.61	3.42	44	BSIZE +YEAR	738.89	48.71
13	WR +BCOND +AGE	693.63	3.44	45	BCOND +YEAR	738.89	48.71
14	WR +BCOND +SEX	693.96	3.77	46	BCOND +SEX	739.11	48.93
15	WR +BSIZE +SEX	694.01	3.82	47	BSIZE +SEX	739.18	48.99
16	WR +BSIZE +BCOND	694.13	3.95	48	BSIZE +BCOND	739.38	49.20
17	WR +AGE +SEX +YEAR	694.39	4.21	49	AGE +SEX +YEAR	739.51	49.32
18	WR +BCOND +SEX +YEAR	694.50	4.32	50	BCOND +SEX +YEAR	739.86	49.67
19	WR +BSIZE +SEX +YEAR	694.59	4.41	51	BSIZE +SEX +YEAR	739.97	49.78
20	WR +BSIZE +AGE +YEAR	695.21	5.03	52	BCOND +AGE +SEX	740.30	50.11
21	WR +BCOND +AGE +YEAR	695.24	5.05	53	BSIZE +AGE +SEX	740.34	50.16
22	WR +BCOND +AGE +SEX	695.28	5.10	54	BCOND +AGE +YEAR	740.43	50.25
23	WR +BSIZE +AGE +SEX	695.31	5.13	55	BSIZE +AGE +YEAR	740.43	50.25
24	WR +BSIZE +BCOND +YEAR	695.45	5.27	56	BSIZE +BCOND +AGE	740.68	50.50
25	WR +BSIZE +BCOND +AGE	695.56	5.38	57	BSIZE +BCOND +YEAR	740.88	50.70
26	WR +BSIZE +BCOND +SEX	695.91	5.72	58	BSIZE +BCOND +SEX	741.11	50.92
27	WR +BCOND +AGE +SEX +YEAR	696.24	6.05	59	BCOND +AGE +SEX +YEAR	741.41	51.23
28	WR +BSIZE +AGE +SEX +YEAR	696.30	6.11	60	BSIZE +AGE +SEX +YEAR	741.51	51.32
29	WR +BSIZE +BCOND +SEX +YEAR	696.39	6.21	61	BSIZE +BCOND +SEX +YEAR	741.86	51.67
30	WR +BSIZE +BCOND +AGE +SEX	697.16	6.98	62	BSIZE +BCOND +AGE +SEX	742.27	52.09
31	WR +BSIZE +BCOND +AGE +YEAR	697.18	7.00	63	BSIZE +BCOND +AGE +YEAR	742.43	52.25
32	WR +BSIZE +BCOND +AGE +SEX +YEAR	698.07	7.89	64	BSIZE +BCOND +AGE +SEX +YEAR	743.40	53.22

3.4 Home range size

Six models explaining home range sie had equivalent AIC values (ΔAIC<2), and all retained the W/R factor (Table 6). However, in none of these models, factor W/R was significant (p>0.05 in all

cases), meaning that overall home range size did not differed between any categories of bird. Indeed, mean size of W and R birds were very similar [mean home range size ± s.e.: W (N=15): 8.40±5.05; R (N=13): 8.10±5.12]

3.5 Home range composition and habitat selection

MANOVA analyses showed that home ranges of migratory and resident birds significantly differed in their habitat composition, but nor in habitat selection within home ranges (Table 7). In addition, habitat composition of the home ranges also differed between study years (Table 4). Differences in habitat composition of the home ranges of W and R birds remained constant between study years, as the migration-by-year interaction term was removed during the backward selection (F=2.19, p=0.079). Differences between W and R birds in habitat composition were due to the higher proportion of riparian vegetation and sparsely wooded areas in W home ranges, but especially to the higher proportions of not-managed olive groves and deciduous wood (Figure 5). R birds had home ranges with a markedly higher percentage of poplar plantations (Figure 5a), and a more homogeneous abundance of the various habitat categories.

Despite of differences in the habitat composition of home ranges, W and R birds showed similar preferences for certain habitat types. For example, both groups selected reed beds of *Arundo donax*, a habitat type scarcely present in the home ranges (~5%), but where over the 10% of the locations were recorded (Figure 5b). In addition, our results indicate that both resident and migratory blackcaps preferred patches of deciduous woods, a habitat type that represented a total of 10-15% of the home ranges, but in which birds were found the 26.26% of the times. In contrast, open areas were avoided by both groups, as well as coniferous woods. Poplar plantations are abundant in the home ranges and used proportionally to their presence by both W and R birds (both values near to 0 in Figure 5b). Overall, habitat selection of migratory and residents Blackcaps is to be considered statistically homogenous (Table 7).

Table 7

MANOVA models testing the factors determining habitat composition of the home ranges (HR) (a) and habitat selection within the home ranges (b) of 30 Blackcaps tracked by radiotelemetry during winter. Non-significant factors were progressively removed from the model. F statistics show the approximate F for Wilk's λ. Bold factors constitute the final model. YEAR= study season 2011 or 2012, WR= migratory or resident individual, AGE= first year vs adult, SEX=male vs female.

(a) Available Habitat within HR

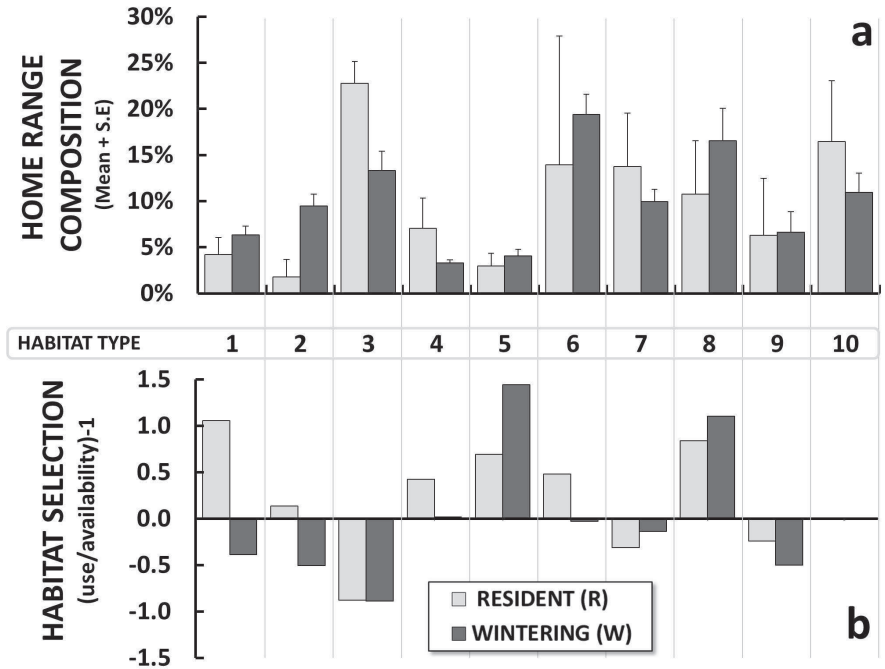
Factor	F	p	p at exclusion
YEAR	**6.245**	**<0.001**	
WR	**2.786**	**0.031**	
AGE	1.723		0.160
SEX	0.707		0.695

(b) Selected Habitat within HR

Factor	F	p	p at exclusion
YEAR	**3.130**	**0.016**	
SEX	0.996		0.475
AGE	0.672		0.724
WR	1.803		0.146

Figure 5

Habitat composition of the home ranges (a) and selection of habitat type within the home ranges (b) by migratory and resident birds. In graph "a", bars indicate mean percentage of home range covered by each habitat type. In graph "b", bars indicate proportion between use and availability of each habitat type within the home range, calculated with the formula [(use/availability)-1]. Zero indicates that habitat type is used proportionally to its presence in the home range. Positive values indicate that habitat type is used more than expected by its presence in the home range, negative values indicate that habitats are avoided. Composition of home ranges differed between W and R birds, while habitat selection did not (see Table 4). Sample sizes are 14 W and 15 R. Habitat types: (1) River and riparian vegetation; (2) Sparsely wooded grasslands; (3) Open areas – scarce or no vegetation; (4) Gardens and orchards; (5) Arundo donax beds; (6) Not-managed olive groves; (7) Managed olive groves; (8) Deciduous wood; (9) Coniferous plantations; (10) Poplar plantations.



4. Discussion

In the Iberian blackcap population we studied, migrants outnumber local breeders by 2.5 to 1 in winter. Migrants, males in particular, are larger than local residents, but all the birds are in similar body condition. Our results provide the first direct evidence that resident and migratory birds aggressively interact, at least in patches with abundant resources. Moreover, we found that larger individuals tend to win these matches. Residents also tend to be dominant over migratory birds, even if mean body size of the latter was bigger and dominance score and body size resulted to be positively correlated. At the same time, dominance status appeared to be negatively related to body conditions. Dominance relationships possibly have consequence on the spatial distribution of the two populations, given that resident and migratory birds have home ranges that differ in habitat composition, being more varied in resident. However, habitat selection did not differ among residents and migrants.

4.1. Composition of the wintering population and consequence on dominance relationships

Some elements of our ecological scenario are similar to those described for a more southern site (Campo de Gibraltar, about 500 Km SW from Cocentaina), which is shared by local resident and northern migratory Blackcaps in winter (Pérez-Tris et al. 1999, Pérez-Tris and Tellería 2002, de la Hera et al. 2007 and 2012). The proportion of migratory birds was very similar (63% in Pérez-Tris et al. 1999 vs 64% in our population), but other features of the population were different. In particular, resident Blackcaps from the Campo de Gibraltar were larger than migratory birds, and within populations, females were larger than males (Pérez-Tris and Tellería 2002). In our study site, resident females were bigger than males, but the opposite pattern was found for migratory birds (Figure 2). Sex-biased differential migration is a common feature in birds (Ketterson and Nolan 1983, Newton 2008), and generally this means that males remain at more northern latitudes than females of the same populations. The large proportion of males in the migratory contingents of Blackcaps in Eastern Spain (Leal et al. 2004, Catry et al. 2006; this study: proportion of males in the overall migratory cohort = 66.12%) suggests that females may migrate further south. This implies that populations of blackcaps from northern Europe would segregate in their Iberian wintering sites. Females from these populations would constitute the biggest individuals in the southern wintering sites, while males from the same populations would constitute the biggest ones at slightly more northern latitudes.

Differences in the relative body size of migratory and resident birds are likely to have important consequences because dominance status is positively related to body size (Figure 3), a general tendency among animals (Brown and Maurer 1986; e.g. reptiles: Tokarz 1985; fishes: Beaugrand et al. 1995; mammals: Haley et al. 1994). The consequence for Iberian breeding populations

is that depending on the composition of the migratory population competition and, as a consequence, the tendency to migrate, will vary. Thus, in our study area, resident birds possibly face a greater challenge than residents from more southern areas (e.g. Gibraltar), because they have to compete with larger-sized males from northern populations. Yet, despite this difference in size, we found that migratory individuals behave as subordinate (Table 5, Figure 4). In other studies, dominance of resident over migratory blackcaps in winter was inferred from habitat segregation: Both in southern France (Berthold 1986) and the Gibraltar area (Pérez-Tris and Tellería 2002, de la Hera et al 2012) resident blackcaps were found in better, more productive habitats than migrants.

The main advantage that residents have over migratory birds is that they are on the site before migratory birds arrive. This is likely to give an advantage to the resident birds by the so-called 'prior residency effect'. This is the probability of the owner of a territory to maintain it during a match (see, for instance, Tobias 1997, Snell-Rood and Cristol 2005). The 'prior residency effect' plays a crucial role in determining the outcome of aggressive interactions, by overriding other important factors (Cristol et al. 1990), like body size. This effect is considered to be one of the main factors explaining the occurrence of partial migration (Kokko 2011), given that different classes of individuals within a population may find it more beneficial than others to maintain a territory during the whole year. In addition, there may be other explanations for the lack of association between size and dominance. For example, body size may be differently reflected in dominance status depending on individual experience (Royle et al. 2005) or on the time of the year (Huntingford et al. 1990). A positive relationship between dominance and experience is a common pattern among birds (e.g. Christol et al. 1990, Barluenga et al. 2000, Jahn et al. 2010b). In our study, experience also may have contributed to determine dominance, as suggested by the selection of "age" among the factors in the best models (Tables 3 and 5), and by the distribution of the mean dominance value shown in Figure 4. However, probably due to low sample size, "age" never reached significance in the models (Table 5).

Body condition of birds was not influenced by age, sex or migratory behaviour, similarly to what was found in the Gibraltar blackcap population, where no relations between these factors and fat storage was found (Pérez-Tris and Tellería 2002). Body condition was, however, was included in the best models explaining dominance score and, surprisingly, was negatively related to this (Figure 3). It is unclear whether dominant birds are in worse body condition because they pay the energetic cost of maintaining a high rank or if, as a consequence of being dominant, they have priority access to food and, therefore, do not need to constitute fat reserves (Matthysen 1990).

4.2 Home ranges composition and habitat selection

Our study area is located in an intensively exploited agricultural landscape, and olive groves constitute over one quarter of the winter home range of both migratory and resident Blackcaps (Figure 5a). Olives are a crucial resources for wintering Blackcaps (Rey 1993), and non-managed olives groves, which host non-harvested fruits, seem to be particularly preferred by wintering bird species (Figure 5b; Assandri et al. 2013). Interestingly, even if habitat composition of migratory and resident winter home ranges differed, all blackcaps seem to use the same resources and habitat types in winter. This finding is in accord with observations made in the populations from Gibraltar, where resident and migratory birds were found in different habitats (Pérez-Tris and Tellería 2002, de la Hera et al. 2012) but have the same diet (Tellería et al. 2013).

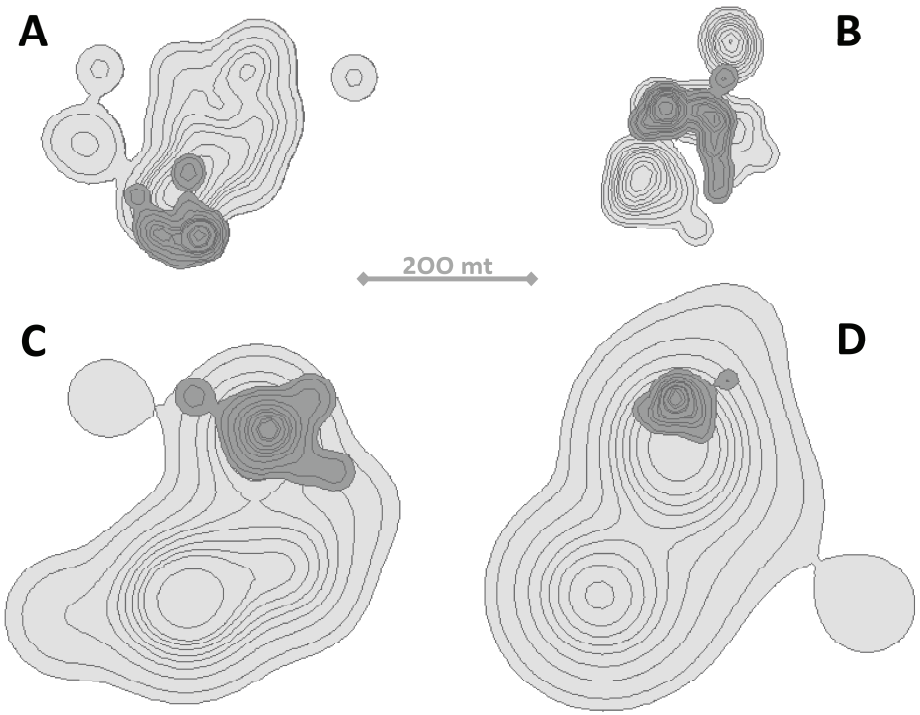
Blackcap generally seem to choose habitats which are advantageous for wintering (e.g. olive groves for feeding and reed beds of *Arundo donax* for roost), but these habitat types are more abundant among home ranges of migratory individuals. Apparently, home ranges of migratory birds are better fitted to wintering requirements, while residents maintain home ranges that include habitat typologies poorly used during winter but may be crucial for breeding, For instance, the higher proportion of poplar plantations and garden and orchards in the home ranges of resident birds (Figure 5) may be interpreted in this sense. This finding may be related to the fact that in highly anthropized areas, as found in our study site, ideal wintering habitats no longer overlap with ideal breeding sites. In well-conserved habitats, as in the Gibraltar area, this may not be the case. There, forests were both the most attractive wintering site, because of the higher variety of fruits, and the best habitat site for Blackcaps (Pérez-Tris and Tellería 2002). The need of residents to maintain, at least, some degree or territoriality during the winter, together with the composition of the home-ranges, less-fitted to the wintering needs, may also explain the negative relation between dominance and body condition we found. The fact that breeding territory and wintering home-range of resident Blackcaps strongly overlap in our population (Figure 6), support the hypothesis that composition of winter home range for this group of birds is influenced by the location of the breeding territory and by the need of maintain it through over the year.

Our results show that there home range size, composition and habitat selection may change among years. Wintering Blackcaps feed on resources that have unpredictable distribution among habitat patches and years (Tellería et al. 2005). However, Blackcaps have strong abilities in fruit tracking (Rey 1995; Tellería and Perez-Tris 2007; Tellería et al. 2008). Therefore, it can be assumed that anomalous abundance of a particular resource between the two study years affected the home range characteristics. In our specific case, we observed that pomegranates (*Punica granatum*), an important food source for Blackcaps, were extremely abundant in 2011 but almost absent in 2012 (pers. obs.). More important than causes of

yearly variation in home range parameters are their consequences. Indeed, our results show that despite among-year variation in availability of certain food, migratory and resident birds responded in the same way, and maintained their differences in the composition of the home ranges (see Results). On the other hand, given the importance of the factor "year" in all models, it is likely that dominance hierarchies change from year to year. We could, however, not study this because we only made behavioural observations in 2012.

Figure 6

Example of home range as obtained by radio telemetry of four resident Blackcaps tracked during both breeding (dark grey) and wintering (pale grey) seasons. Lines identify intervals of 10% of the total home range. A: adult male; B and C: first year males; D: adult female.



4.3 Does Winter competition explain the unusual pattern of partial migration in the local breeding population?

The observation that females tend to have lower dominance scores and are almost absent in the resident population in winter suggests sex-mediated partial migration in the local breeding population, in which females are more likely to migrate. Differences in migratory behaviour between sexes are probably common among short distance migrants (Fudickar et al. 2013). However, determinants of partial migration are generally more complex than just sex. Indeed, even if the control of partial migration is considered to be mainly endogenous, the role of external environmental factors in determining the migratory status of a certain individual had been recently re-evaluated (Pulido 2011). In a partially migratory Blackcap population from southern France, Berthold (1986) demonstrated using common-garden experiments that males had a genetical predisposition that made them more likely to become resident. They further proposed that their ability to outcompete northern migratory birds enhanced the probability for adult and males to behave as resident. Our results partially agree with this scenario, supporting the hypothesis of a dominance-determined partial migration, reflected in a biased frequency of migrants among different sex and age groups. However, the observation of a higher ratio of residents among first-years birds apparently contradicts this hypothesis, because first-year birds are expected to be subordinate relative to adults (Gautheraux 1978, Ketterson and Nolan 1983, Greenberg 1986). We argue that this pattern may be caused by the different cost-benefit balances of migration between adults and juveniles. The strength of the prior-residency effect possibly makes it particularly beneficial for adult males to maintain a territory throughout the year (Kokko 2011, see also 4.1 above). Winter territoriality in blackcaps is very likely, given that full songs are commonly heard in our study area in mid-winter (pers. obs.). In contrast, adult females and adults of small size have no chance of winning competitive interactions with northern migrants. Yet, these birds may have a good chance to become dominant in southern wintering quarters where northern conspecifics are absent, so that cost-benefit balance would make migration beneficial to them. Juveniles are exposed to different pressures, given that they are likely to be subordinate at any site. For them, the best strategy would be thus to save, at least, the cost of migration and stay in their natal area. Moreover, migration tends to be more risky for less experienced birds (Berthold 2001, Newton 2008), so that differences in the response to weather conditions encountered en-route have been observed between juveniles and adults (e.g. Morganti et al. 2011). The theoretical model proposed by Taylor and Norris (2007, see their Figure 2a) shows that for birds that suffer high mortality during migration, the most likely strategy is residency, even if this entails increased risk of mortality due to competition (as expected for low-ranked juveniles). Moreover, the degree of aggressiveness between adults and juveniles is possibly lower than among adults. Natural selec-

tion has favoured mechanisms that prevent aggressive interactions with adult conspecifics, as delayed plumage maturation or delayed reproduction (Berggren et al. 2004, Vergara and Fargallo 2007, Hawkins et al. 2012).

We found no other study in literature reporting the same eco-evolutionary scenario of partial migration that we describe here, in which some classes of adults migrate, while most of juveniles and top-ranked adults remain. However, some analogy with our system can be found among partial migrant birds from the tropics, where birds higher in rank (in those cases adult males) where more likely to migrate than birds from supposedly subordinate categories (Boyle 2008, Jahn et al. 2010b). Tropical partial migratory birds from living in the rainforests mainly differ from the ones at northern or temperate latitudes in the fact that food shortage and temperature are not the main limiting factors determining the occurrence of migration (Boyle 2008, Jahn et al. 2010b). In this sense, the case of Blackcaps breeding in eastern and southern Spain may be more similar to tropical systems than to those ones from northern Europe, given that availability of food in winter may not be a limiting factor for this species in this area (Tellería et al. 2013). This scenario needs to be further validated through a better assessment of the role of yearly variation in food availability in determining the strength of competitive relationships. Trade-offs between costs and benefits of migration for the different classes of individuals may strongly oscillate between years if the degree of aggressiveness changes with changes in the availability and abundance of different food resources.

4.4 Consequences and future scenarios facing climate change

The progressive reduction of migratory distances in northern and central European Blackcaps (see, Pulido and Berthold 2010) may have the effect to reduce competition in southern European populations in winter. Consequently, residency is expected to be favoured among locally breeding birds. This change in selection, favouring residency, is expected not only in Blackcaps but in all European intra-Palearctic migrants that are shortening migratory distance (see Visser et al. 2009, Lehikoinen et al. 2013). Yet, another prediction is that populations of Blackcaps, mostly from the most northern breeding populations, that used to winter south of the Sahara will start to overwinter in the Mediterranean basin, as we found in trans-Saharan birds (Section I of the thesis). This would increase competition with local residents. Overall, local populations will probably be exposed to contrasting selective pressures that on the one hand favour residency via reducing competition with migratory conspecifics from central-northern populations and possibly ameliorating winter conditions, but increase competition with northern populations of trans-Saharan migrants that are starting to winter in Mediterranean.

Making predictions is further complicated because of the effects of climate change on other factors (as availability of some resources), which may confound the effects of winter amelioration

and competition. This was recently demonstrated in a partially migratory Swedish blue tit (*Cyanistes caeruleus*) population, in which the frequency of migrants unexpectedly increased during a period of climatic warming (Nilsson et al. 2006).

Supplementary materials

Annex 1

Complete list of the 363 references from which data about wintering records of European trans-Saharan species were gathered.

ADENEX, Aves de Extremadura. Vol 2. Anuario ADENEX 1999-2000. 2001, Mérida.

Aixerreku, Anuario Ornitológico Urdaibai 96. 1997: Gobierno Vasco.

Alberto, L.J. and F.J. Purroy, Censos de limicolas invernantes en españa (1978, 79 y 80), realizados por la sociedad española de Ornitologia Ardeola, 1981. 28: p. 3-34.

Alegre-Alonso, J. and A. Hernandez-Lazaro, La comunidad ornitica de la laguna de Santiz (Valdepolo, León), parametros ecologicos. Oxyura, 1989. 5(1): p. 61-82.

Álvarez, J.A., et al., Áreas de concentración post-nupcial, invernal y primaveral de la cigüeña negra (Ciconia nigra) en Extremadura Alytes, 1993. VI: p. 51-64.

Amat, J.A. and L. García, Distribución y fluctuaciones mensuales de aves acuáticas en Andalucia Occidental. Invierno 1977-78. Doñana - Acta vertebrata, 1979. 6(1): p. 77-90.

Andrada, J. and A. Franco, Sobre el área de invernada de Falco naumanni en españa. Ardeola, 1975. 21(1): p. 321-24.

Anonimo, Noticiario Ornitológico, 1981. Ardeola, 1981. 28(1): p. 149-65.

Anonimo, Noticiario Ornitológico, 1983. Ardeola, 1983. 29(1): p. 176-93.

Anton, M., Anuari d'Ornitologia de Catalunya. 2007. 2008, Barcelona: Institut Català d'Ornitologia.

Arratibel, P., et al., Anuario Ornitológico de Navarra, Vol.1 1993-1994. 1995, Pamplona: GOROSTI.

Arratibel, P., et al., Anuario Ornitológico de Navarra, Vol.2. 1996, Pamplona: GOROSTI.

Arratibel, P., et al., Anuario Ornitológico de Navarra 1996, Vol.3. 1998a, Pamplona: GOROSTI.

Arratibel, P., et al., Anuario Ornitológico de Navarra 1997, Vol.4. 1998b, Pamplona: GOROSTI.

Arratibel, P., et al., Anuario Ornitológico de Navarra 1998, Vol.5. 2000, Pamplona: GOROSTI.

Arratibel, P., et al., Anuario Ornitológico de Navarra 1999, Vol.6. 2001, Pamplona: GOROSTI.

Arratibel, P., et al., Anuario Ornitológico de Navarra 2000-2001. Vol.7. 2007, Pamplona: GOROSTI.

Asociación de Amigos de los Humedales del Sur de Alicante, Censo de Aves Acuáticas Invernantes el los pp.nn. del sur de Alicante. Enereo de 1995. La Matruca, 1995. 1: p. 6-7.

Asociación de Amigos de los Humedales del Sur de Alicante, Noticiario Ornitológico. La Matruca, 1995. 2: p. 10.

Asociación de Amigos de los Humedales del Sur de Alicante, Noticiario Ornitológico. La Matruca, 1996. 4: p. 9.

Asociación de Amigos de los Humedales del Sur de Alicante, Crónica Ornitológica 2004. La Matruca, 2007. 17: p. 27-39.

Asociación de Amigos de los Humedales del Sur de Alicante, Crónica Ornitológica 2005. La Matruca, 2008. 18: p. 43-59.

Aymí, R. and S. Herrando, Anuari d'Ornitologia de Catalunya. 2000. 2003, Barcelona: Institut Català d'Ornitologia.

Aymí, R. and S. Herrando, Anuari d'Ornitologia de Catalunya. 2001. 2005, Barcelona: Institut Català d'Ornitologia.

Barragán, A., et al., Anuario Ornitológico de la provincia de Sevilla: años 2000-2005. 2008, Sevilla: GOSUR.

Barros, Á. and P. Galán, V Anuario das Aves de Galicia, 1997. 2000, A Coruña: Barros, A & Galán, P.

Bermejo, A., et al., Censo general (enero, 1984) de gaviotas y charranes (Aves Laridae) invernantes en la Península Ibérica con especial referencia a las zonas de invernada. Asturnatura, 1985. 4.

Bermejo, A., J. De la Puente, and J. Seoane, Anuario Ornitológico de Madrid 2000. 2001, Madrid: SEO-Monticola.

Bermejo, A., J. De la Puente, and J. Seoane, Anuario Ornitológico de Madrid 2001. 2002, Madrid: SEO-Monticola.

Bernis-Madrazo, F., Aves migradoras ibericas. 1966, Madrid: SEO/Birdlife.

Bernis-Madrazo, F., La migración de las aves en el estrecho de Gibraltar. Vol I: Aves planeadoras. 1980, Madrid: Universidad Complutense.

Bernis-Madrazo, F. and F. Bernis-Carro, Breve Comentario sobre invernada de aves en la cuenca del ebro (enero 1962). Ardeola, 1963. 8: p. 228-31.

Blanco, M., Anuario Ornitológico de la provincia de Salamanca, 1924-2003 2004: SEO-Salamanca.

Blanco, M., Anuario Ornitológico de la provincia de Salamanca, 2004-2006. 2007: SEO-Salamanca.

Blondel, J. and C. Blondel, Remarques sur l'hivernage des Limicoles et autres oiseaux aquatiques au Maroc (Janvier 1964). Alauda, 1964. 32(4): p. 250-279.

Bort, J.L.C., Anuario Ornitológico de Castellón 2004, Vol.2. 2007, Castellón: http://www.internatura.org/aocs.

Bort, J.L.C., Anuario Ornitológico de Castellón 2007. Vol.5. 2009, Castellón: http://www.internatura.org/aocs.

Bueno, A., Rocín - Anuario Ornitológico de Aragón 1999-2003. 2004, Zaragoza: SEO-Aragón.

Cabot, J., et al., Status de la pagaza piquirroja (Hydropogne caspia) en el SO español. Doñana - Acta vertebrata (Notas), 1984. 11(1): p. 146-49.

Canto, J.L., Noticiario de Fauna Vertebrada del Parque Natural 2004-2005. IBERIS-Revista per al coneixement dels ecosistemes del carrascal de la Font Roja, 2006. 4: p. 113-140.

Casas, F., A. Arredondo, and J. López-Jamar, Anuario Ornitológico de Ciudad Real 2004-2005. 2007, Ciudad Real: SEO-Ciudad Real.

Cherkaoui, I., et al., Quelques observation d'oiseaux rares ou peu communs en hiver 2005-2006 à l'embouchure de la Moulouya et dans la plaine de Triffa (nord-est du Maroc). Go-South Bullettin, 2006. 3: p. 43-47.

COA, Anuario Ornitológico Asturiano 1993. El Draque, revista de la Coordinadora Ornitolóxica d'Asturies. 1996.

COA, Anuario Ornitolóxicu d'Asturies, 1994 y 1995. El Draque, revista de la Coordinadora Ornitolóxica d'Asturies. Vol. 2. 1997. 61-255.

Conde Teira, M.A. and G. Lijó Pose, X Anuario das Aves de Galicia, 2002. 2006, Santiago de Compostela: Sociedade Galega de Ornitoloxía.

Copete, J.L., Anuari d`ornitologia de Catalunya, 1996. 1998, Barcelona: Group Catalá d'Anellament.

Copete, J.L., Anuari d'Ornitologia de Catalunya, 1997. 2000, Barcelona: Grup Catalá d'Anellament.

Costa, H., et al., Aves de occorrencia rara ou acidental em Portugal. Pardela, 2000. 11: p. 4-18.

Costa, L., Avifauna en pinares de Doñana. Doñana - Acta vertebrata, 1984. 11(2): p. 151-83.

Costa, L.T. and R. Rui, Contagens de aves aquáticas em Portugal Janeiro de 1994. AIRO, 1994. 5(1): p. 8-16.

Costa, L.T. and R. Rui, Contagens de aves aquáticas em Portugal Janeiro de 1997. AIRO, 1997. 8(1/2): p. 25-32.

Dakki, M., et al., Recensement Hivernal d'Oiseaux d'eau au Maroc: 1996-2000. Travaux de l'Institut Scientifique. 2002, Rabat: Université Mohammed V-Agdal, Institut Scientifique.

De Juana, E., Datos invernales sobre aves de Marruecos (Diciembre 1973). Ardeola, 1974. 20: p. 267-286.

De Juana, E., Noticiario Ornitológico, mar 1984. Ardeola, 1984. 30(1): p. 115-24.

De Juana, E., Noticiario Ornitológico, junio 1984. Ardeola, 1984. 31(2): p. 141-47.

De Juana, E., Noticiario Ornitológico, 1985. Ardeola, 1985. 32(2): p. 409-24.

De Juana, E., Noticiario Ornitológico, 1986. Ardeola, 1986. 33(1-2): p. 203-13.

De Juana, E., Noticiario Ornitológico, 1987. Ardeola, 1987. 34(2): p. 275-92.

De Juana, E., Noticiario Ornitológico, 1988. Ardeola, 1988. 35(2): p. 297-316.

De Juana, E., Noticiario Ornitológico, 1989. Ardeola, 1989. 36(2): p. 231-64.

De Juana, E., Noticiario Ornitológico, 1990. Ardeola, 1990. 37(2): p. 325-52.

De Juana, E., Noticiario Ornitológico, 1991. Ardeola, 1991. 38(2): p. 327-50.

De Juana, E., Noticiario Ornitológico, 1993. Ardeola, 1993. 40(1): p. 87-104.

De Juana, E., Noticiario Ornitológico, Junio 1994. Ardeola, 1994a. 41(1): p. 91-102.

De Juana, E., Noticiario Ornitológico, dec 1994. Ardeola, 1994b. 41(2): p. 193-202.

De Juana, E., Noticiario Ornitológico, 1995. Ardeola, 1995. 42(2): p. 211-31.

De Juana, E., Noticiario Ornitológico, 1996. . Ardeola, 1996. 43(2): p. 239-59.

De la Puente, J., A. Bermejo, and J. Seoane, Anuario Ornitológico de Madrid 1996. 1997, Madrid: SEO-Monticola.

De la Puente, J., A. Bermejo, and J. Seoane, Anuario Ornitológico de Madrid 1997. 1998, Madrid: SEO-Monticola.

De la Puente, J., A. Bermejo, and J. Seoane, Anuario Ornitológico de Madrid 1998. 1999, Madrid: SEO-Monticola.

De la Puente, J., A. Bermejo, and J. Seoane, Anuario Ornitológico de Madrid 1999. 2000, Madrid: SEO-Monticola.

de la Puente, J. and E. de Juana, Noticiario Ornitológico, 1997. Ardeola, 1997. 44(2): p. 243-61.

de la Puente, J., et al., Noticiario Ornitológico, 2002. . Ardeola, 2002. 49(1): p. 173-94.

De la Puente, J. and J.A. Lorenzo, Noticiario Ornitológico, 2000. Ardeola, 2000. 47(1): p. 161-70.

de la Puente, J. and J.A. Lorenzo, Noticiario Ornitológico, 2001. Ardeola, 2001. 48(1): p. 137-47.

de la Puente, J., J.A. Lorenzo, and E. de Juana, Noticiario Ornitológico, junio 1998. Ardeola, 1998a. 45(1): p. 117-28.

de la Puente, J., et al., Noticiario ornitológico, junio 2003. Ardeola, 2003. 50(1): p. 151-69.

De la Puente, J., J. Pérez-Tris, and A. Bermejo, Anuario Ornitológico de Madrid 2002. 2003, Madrid: SEO-Monticola.

De la Puente, J., et al., Anuario Ornitológico de Madrid 2003. 2004, Madrid: SEO-Monticola.

De la Puente, J., et al., Anuario Ornitológico de Madrid 2004. 2005, Madrid: SEO-Monticola.

De la Puente, J., et al., Anuario Ornitológico de Madrid 2005. 2006, Madrid: SEO-Monticola.

De la Puente, J., et al., Anuario Ornitológico de Madrid 2006. 2007, Madrid: SEO-Monticola.

de la Puente, J., J. Pinilla, and J.A. Lorenzo, Noticiario Ornitológico, dic 1998. Ardeola, 1998b. 45(2): p. 241-53.

de la Puente, J., J. Pinilla, and J.A. Lorenzo, Noticiario Ornitológico, 1999 (1). Ardeola, 1999a. 46(1): p. 149-62.

de la Puente, J., J. Pinilla, and J.A. Lorenzo, Noticiario ornitologico 1999 (2). Ardeola, 1999b. 46(2): p. 305-14.

De Lope, F., La avifauna de las Vegs Bajas de Guadiana. Doñana - Acta vertebrata, 1983. 10(1): p. 91-121.

De Souza, J.A., et al., IV Anuario das Aves de Galicia, 1996. 1998, A Coruña: GRUPO NATURALISTA HÁBITAT.

Del Moral, J.C., et al., Atlas de las aves invernantes de Madrid 1999-2001. 2002, Madrid: SEO-Birdlife y Comunidad de Madrid.

Del Moral, J.C., et al., Atlas de las aves invernantes de Madrid 1999-2001. 2002, Madrid: SEO-Monticola y Comunidad de Madrid.

Diez, P.M., P. De Leon, and R. Saez-Royuela, Aves invernantes en los estanques de la casa de campo. Ardeola, 1955. 2: p. 23-30.

Diéz-Ponce de Leon, P.M., Sobre la posible invernada de (Cyanosilvia svecica) en el centro de España. Ardeola, 1959. 5(1): p. 207.

Diputació Provincial de Tarragona - Comissió de Defensa del Medio Ambient, Butletí del Parc Natural delta de L'Ebre, n.3, Diciembre 1988. 1988, Tarragona.

Diputació Provincial de Tarragona - Comissió de Defensa del Medio Ambient, Butlletí del Parc Natural delta de L'Ebre Nº4, Diciembre 1989. 1989, Tarragona.

Diputació Provincial de Tarragona - Comissió de Defensa del Medio Ambient, Butlletí del Parc Natural delta de L'Ebre Nº5, Diciembre 1990. . 1990, Tarragona.

Diputació Provincial de Tarragona - Comissió de Defensa del Medio Ambient, Butlletí del Parc Natural delta de L'Ebre Nº6, Diciembre 1991. . 1991, Tarragona.

Diputació Provincial de Tarragona - Comissió de Defensa del Medio Ambient, Butlletí del Parc Natural delta de L'Ebre Nº7, Diciembre 1992. . 1992, Tarragona.

D'Oliveira, M.P., Aves da Península Iberica e especialmente de Portugal. 1930, Coimbra: Universidade de Coimbra.

Dubois, P. and L. Duhautois, Notes sur l'Ornithologie Marocaine. Alauda, 1977. 45(4): p. 285-291.

El Ghazi, A. and J. Franchimont, Chronique ornithologique du G.O.MAC. pour 1996 - Parte I: des grebes aux pics. Porphyrio, 1997. 9(1/2): p. 70-164.

El Ghazi, A. and J. Franchimont, Chronique ornithologique du G.O.MAC. pour 1996 - Parte II: des alouettes aux bruants. Porphyrio, 1998-99. 10-11(1/2): p. 25-59.

El Ghazi, A., J. Franchimont, and T. Moumni, Chronique ornithologique du G.O.MAC. pour 1997. Porphyrio, 1998-99. 10-11(1/2): p. 60-253.

Elias, G., Observaçoes Ornitológicas. Pardela, 2000. 12: p. 20-23.

Elias, G., Noticiário Ornitológico, 2001. Anuário Ornitológico (Portugal), 2003. 1: p. 37-46.

Elias, G., Noticiário Ornitológico, 2002. Anuário Ornitológico (Portugal), 2004. 2: p. 21-54.

Elias, G., Noticiário Ornitológico, 2003. Anuário Ornitológico (Portugal), 2005. 3: p. 23-53.

Elias, G., Noticiário Ornitológico, 2004. Anuário Ornitológico (Portugal), 2006. 4: p. 17-54.

Elias, G., et al., Aves de ocorrência rara ou acidental em Portugal, ano 2002. Anuário Ornitológico, 2004. 2: p. 1-20.

Elias, G.L., et al., Atlas das aves invernantes do Baixo Alentejo. 1998, Lisboa: SPEA-Birdlife.

Elias, G.L., et al., Atlas das Aves Invernantes do Baixo Alentejo. (Coords.) 1998, Lisboa: Sociedade Portuguesa para Estudo das Aves.

Ena, Y. and F.J. Purroy, Evolución demografica de Anatidas y Fochas invernantes entre 1972-1980. Alytes, 1983. 1: p. 131-138.

Enciso, J.P. and M. Paracuellos, Dináminca estacional de la comunidad de aves acuáticas en los humedales del levante almeriense (SE ibérico). Caracterización e importancia ornítica provincial. Oxyura, 1997. 9(1): p. 29-43.

Epifanio, J.C. and C. Vidal, XII Anuario das Aves de Galicia, 2004. 2008, Santiago de Compostela: Sociedade Galega de Ornitoloxía.

Escandell Salom, A., Censos Anuals d'Aus Aquátiques i Marines a Menorca. Socarrell - Butlleti divulgatio del G.O.B a Menorca - Estiu 1986, 1986. 6: p. 20-21.

Estacio Ornitologica L'Albufera, Anuario Ornitológico Comunidad Valenciana, 1988. 1989, Valencia.

Estacio Ornitologica L'Albufera, Anuario Ornitológico Comunidad Valenciana, 1989. 1990, Valencia.

Estacio Ornitologica L'Albufera, Anuario Ornitológico Comunidad Valenciana, 1990. 1991, Valencia.

Estacio Ornitologica L'Albufera, Anuario Ornitológico Comunidad Valenciana, 1991. 1992, Valencia.

Estacio Ornitologica L'Albufera, Anuario Ornitológico Comunidad Valenciana, 1992. 1993, Valencia.

Estacio Ornitologica L'Albufera - SEO, Anuario Ornitológico Comunidad Valenciana, 1993. 1994, Valencia.

Estacio Ornitologica L'Albufera/ SEO-BirdLife, Anuario Ornitológico Comunidad Valenciana, 1994. 1997, Valencia.

Estacio Ornitologica L'Albufera/ SEO-BirdLife, Anuario Ornitológico Comunidad Valenciana, 1995-1997. 2000, Valencia.

Estación Biológica de Doñana. http://www-rbd.ebd.csic.es/Seguimiento/mediobiologico.htm. 2009 20-07-2009].

Estrada, J. and M. Anton, Anuari d'ornitologia de Catalunya. 2006. 2007, Barcelona: Institut Català d'Ornitologia.

Estrada, V., F. Latre, and A. Julien, Dades hivernals de Xot Otus scops i Colltort Jynx Torquilla a Catalunya i Baleares (1975-1983). Buttletí del Grup Catalá d'Anellament, 1985. 4: p. 8-12.

Fareh, M., Chronique ornithologique du G.O.MAC. pour 2004. http://perso.menara.ma/gomac/, 2005.

Fareh, M., Chronique ornithologique du G.O.MAC. pour 2005. http://perso.menara.ma/gomac/, 2006.

Feith, H., Projecto Chegadas - Relatorio 2008. 2008, Lisboa: SPEA.

Feith, H., Projecto Chegadas - Relatorio 2009. 2009, Lisboa: SPEA.

Fernández, F.J. and Fernandéz-Arroyo, Hoja informativa sobre el refugio de rapces de Montejo. Nº19, Marzo 1992. 1992.

Finlayson, C., Birds of the strait of Gibraltar. 1992, London: Poyser Ltd.

Franchimont, J., Chronique Ornithologique 1989/1 - Janvier a Mars. Porphyrio, 1989. 1(1/2): p. 9-22.

Franchimont, J., M.S. Chahlaoui, and A. Sayad, Analyse de l'evolution des effectives des oiseaux d'eau hivernantes dans le Maroc Central au cours de la décennie 1983-93. Porphyrio, 1994. 6(1): p. 7-94.

Franchimont, J., A. Sayad, and J. Boutammachte, Recensement Hivernal des Oiseaux d'Eau au Maroc en Janvier 1991. Porphyrio, 1991. 3(1/2): p. 20-36.

Gainzarain, J.A., Atlas de las aves invernantes en Álava (2002-2005). 2006, Vitoria-Gasteiz: Diputación Foral de Álava.

Gámez, I., et al., Anuario Ornitológico de La Rioja 1993-1997. 1999, Logroño: Ecologistas en Acción de La Rioja.

Gámez, I., et al., Anuario Ornitológico de La Rioja 1998-2000. 2002, Logroño: Club Ornitológico de La Rioja.

Garcia Cordoba, J., Avifauna del Concejo de Piloña en 1975. Asturnatura, 1977. III: p. 96-104.

García Sánchez, E., Annuariu Ornitolóxicu d'Asturies, 1996. El Draque, revista de la Coordinadora Ornitolóxica d'Asturies, 1998. 3: p. 13-158.

García Sánchez, E., Annuariu Ornitolóxicu d'Asturies, 1997. El Draque, revista de la Coordinadora Ornitolóxica d'Asturies, 2003. 4: p. 27-234.

García Sánchez, E., Annuariu Ornitolóxicu d'Asturies, 1998. El Draque, revista de la

Coordinadora Ornitolóxica d'Asturies, 2004. 5: p. 15-198.

García Sánchez, E., Annuariu Ornitolóxicu d'Asturies, 1999. El Draque, revista de la Coordinadora Ornitolóxica d'Asturies, 2006. 6: p. 15-198.

García Sánchez, E., et al., Annuariu Ornitolóxicu d'Asturies, 2000. El Draque, revista de la Coordinadora Ornitolóxica d'Asturies, 2007. 7: p. 35-255.

Garrido, G.H., Anuario Ornitologico de Doñana, nº0, Diciembre 2000. 2000, Estación Biológica de Doñana: Consejo Superior de Investigaciones Cientificas.

Garrido , G.H., Anuario Ornitológico de Doñana, nº1 (Sep 1999 - Ago 2001). 2002, Estación Biológica de Doñana: Consejo Superior de Investigaciones Cientificas.

Generalitat de Catalunya - Departament d'Agricultura Ramdeira i Pesca, Butletí del Parc Natural Delta de L'Ebre Nº9, 1995-1996. . 1996, Tarragona.

Generalitat de Catalunya - Departament d'Agricultura Ramdeira i Pesca, Butletí del Parc Natural Delta de L'Ebre Nº10, 1997-1998. . 1998, Tarragona.

Gibraltar Ornithological Group, The bullettin of the Gibraltar Ornithological Group. Vol 1, N.1. 1976a, Gibraltar.

Gibraltar Ornithological Group, The bulletin of the Gibraltar ornithological group. Vol.1 Nº2. 1976b, Gibraltar.

Gibraltar Ornithological Group, The bulletin of the Gibraltar ornithological group. Vol 2.Nº1. 1977, Gibraltar.

Gil, H.V., El naturalista indomito. Boletín para la divulgación, estudio y conservación de la naturaleza en la región de Murcia. Junio 1997, n.5. Vol. 5. 1997, Murcia: ANSE-delegación local de Murcia.

Gil, H.V., El naturalista indomito. Boletín para la divulgación, estudio y conservación de la naturaleza en la región de Murcia. Diciembre 1997, n.6. Vol. 6. 1997, Murcia: ANSE-delegación local de Murcia.

Gil, H.V., El naturalista indomito. Boletín para la divulgación, estudio y conservación de la naturaleza en la región de Murcia. Febrero 1998, n.7. 1998, Murcia: ANSE-delegación local Murcia.

Gil, H.V., El naturalista indomito. Boletín para la divulgación, estudio y conservación de la naturaleza en la región de Murcia. Abril 1998, n.8. Vol. 8. 1998, Murcia: ANSE-delegación local Murcia.

Gil, H.V., El naturalista indomito. Boletín para la divulgación, estudio y conservación de la naturaleza en la región de Murcia. Mayo 1999, n.11. Vol. 11. 1999, Murcia: ANSE-delegación local Murcia.

Gil, H.V., El naturalista indomito. Boletín para la divulgación, estudio y conservación de la naturaleza en la región de Murcia. Marzo 1999, n10. Vol. 10. 1999, Murcia: ANSE-delegación local Murcia.

Gil, H.V., El naturalista indomito. Boletín para la divulgación, estudio y conservación de la naturaleza en la región de Murcia. Diciembre 1999, n.12. Vol. 12. 1999, Murcia: ANSE-delegación local de Murcia.

Gil, H.V., El naturalista indomito. Boletín para la divulgación, estudio y conservación de la naturaleza en la región de Murcia. Abril 2000, n.13. Vol. 13. 2000, Murcia: ANSE-delegación local de Murcia.

Gil, R., A.N.S.E. Boletín informativo mensual n.95, Mayo 1990, de la asociación de naturalistas del sureste. 1990, Murcia: ANSE-delegación local de Murcia.

Gil, V.H., El naturalista indomito. Boletín para la divulgación, estudio y conservación de la naturaleza en la región de Murcia. Octubre 1996, n.3. Vol. 3. 1996, Murcia: ANSE-delegación local de Murcia.

González, D., et al., Anuario Ornitológico de la Provincia de Burgos. Volumen I. 2006, Burgos: Caja de Burgos. Aula de Medio Ambiente.

González-López, A.J., Resumen de los censos de aves acuáticas en la provincia de Albacete. La Calandria, 1998. 6: p. 28-29.

Gorospe, G., Urtekari Ornitologikoa - Anuario Ornitológico GIPUZKOA 1990. 1991, Donostia: Sociedad Oceanográfica de Gipuzkoa.

Gorospe, G., Urtekari Ornitologikoa - Anuario Ornitológico GIPUZKOA 1991. 1993, Donostia: Departamento de Economia, Planificación y Medio Ambiente - Gobierno Vasco.

Gorospe, G., Urtekari Ornitologikoa - Anuario Ornitológico GIPUZKOA 1993. 1995, Donostia: ITSAS ENARA - ORNITOLOGI ELKARTEA.

Gorospe, G., Urtekari Ornitologikoa - Anuario Ornitológico GIPUZKOA 1994. 1996a,

Donostia: ITSAS ENARA - ORNITOLOGI ELKARTEA.

Gorospe, G., Urtekari Ornitologikoa - Anuario Ornitológico GIPUZKOA 1995. 1996b, Donostia: Departamento de Ordenación del Territorio, Vivienda y Medio Ambiente - Gobierno Vasco.

Gorospe, G., Urtekari Ornitologikoa - Anuario Ornitológico GIPUZKOA 1996. 1997, Donostia: ITSAS ENARA - ORNITOLOGI ELKARTEA.

Gorospe, G., Urtekari Ornitologikoa - Anuario Ornitológico GIPUZKOA 1997. 1998, Donostia: Departamento de Ordenación del territorio, vivienda y medio ambiente - Gobierno Vasco.

Gorospe, G., Urtekari Ornitologikoa - Anuario Ornitológico GIPUZKOA 1998. 2000, Donostia: Departamento de Ordenación del territorio, vivienda y medio ambiente - Gobierno Vasco.

Gorospe, G., Urtekari Ornitologikoa - Anuario Ornitológico GIPUZKOA 1999 - 2000. 2001, Donostia: Departamento de Ordenación del territorio, vivienda y medio ambiente - Gobierno Vasco.

Gragera Diaz, F., Nuevas localidades de invernada del cernicalo primilla (Falco naumanni) en Extremadura. Boleta - Boletin del Grupo Iberico de Rapaces., 1992. 5, primavera 1992.

Grup Balear d'Ornitologia, Anuari Ornitológic,1985-1986. Vol. 1. 1987, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic, 1987. Vol. 2. 1988, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 1988. Vol. 3. 1989, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitólogic de les Baleares, 1989. Vol. 4. 1990, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 1990. Vol. 5. 1991, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 1991. Vol. 6. 1992, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 1992. Vol. 7. 1993, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 1993. Vol. 8. 1994, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 1994. Vol. 9. 1995, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 1995. Vol. 10. 1996, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 1996. 1997, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 1997. 1998, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 1998. 1999, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 1999. 2000, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 2000. Vol. 15. 2001, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 2001. 2002, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 2002. 2003, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 2003. Vol. 18. 2004, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 2004. Vol. 19. 2005, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitologic de les baleares, 2005. Vol. 20. 2006, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 2006. Vol. 21. 2007, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 2007. VOL 22. 2008, Palma de Mallorca.

Grup Balear d'Ornitologia, Anuari Ornitológic de les Baleares, 2008 VOL.23. 2009, Palma de Mallorca.

Grup Catalá d'Anellament, Noticiari Ornitológic de Catalunya, 1988-1989. 1990, Badalona.

Grup d'Estudi i Defensa de la Natura, Boletín Circular de Agró 0-1. 1986, Valencia.

Grupo de Trabalho Raridades, Noticiário Ornitológico. Pardela, 1996A. 2(1): p. 18-19.

Grupo de Trabalho Raridades, Noticiário Ornitológico. Pardela, 1996B. 2(2): p. 21-23.

Grupo de Trabalho Raridades, Noticiário Ornitológico. Pardela, 1997. 6: p. 21-22.

Grupo de Trabalho Raridades, Noticiário Ornitológico. Pardela, 1998. 7: p. 16-20.

Grupo de Trabalho Raridades, Noticiário Ornitológico. Pardela, 1999 A. 9: p. 22-23.

Grupo de Trabalho Raridades, Noticiário Ornitológico. Pardela, 1999 B. 10: p. 21-23.

Grupo Iberico de Rapaces, Primer censo invernal de rapaces. Avance de los resultados. Boleta - Boletin del Grupo Iberico de Rapaces., 1991a. 2, primavera 1991.

Grupo Iberico de Rapaces, Primer censo invernal de rapaces. Invierno 1990-91. Boleta - Boletin del Grupo Iberico de Rapaces., 1991b. 4, otoño 1991.

Grupo Ornitológico Malaca, Anuario Ornitológico de Málaga,1993. 1994, Malaga.

Guardiola, A.e. Anuario Ornitológico de la Región de Murcia. Informe 1/2003. . 2004a.

Guardiola, A.e. Anuario Ornitológico de la Región de Murcia. Informe 1/2004. . 2004b.

Guardiola, A.e. Anuario Ornitológico de la Región de Murcia. Informe 2/2004. . 2004c.

Guardiola, A.e. Anuario Ornitológico de la Región de Murcia. Informe 3/2004. . 2004d.

Guardiola, A.e. Anuario Ornitológico de la Región de Murcia. Informe 4/2004. . 2004e.

Guardiola, A.e. Anuario Ornitológico de la Región de Murcia. Informe 1/2005. . 2006.

Guardiola, A.e. Anuario Ornitológico de la Región de Murcia. Informe 2/2006. . 2007.

Guardiola, A.e. Anuario Ornitológico de la Región de Murcia. Informe 1/2007. . 2007b.

Instituto nacional de metereología - Sección de meteorología agraria, Fenologia de aves para españa. 1982, Madrid: Ministerio de Transportes, Tursimo y Comunicaciones.

internatura.org, Anuario Ornitológico de Castellón, 2003. 2005, Castellón.

Isenmann, P., Note sur les stationnements de larides sur la cote Atlantique du Maroc en décembre 1976. Bulletin de l'Institut Scientifique, Rabat, 1978. 2: p. 77-86.

Jara, J., et al., Aves de ocorrência rara ou acidental em Portugal, ano 2005. Anuário Ornitológico, 2007. 5: p. 1-34.

Jara, J., et al., Aves de ocorrencia rara ou acidental em Portugal. (2006 e 2007). Anuário Ornitológico, 2008. 6: p. 1-45.

Jay-Fayez, A., J. Franchimont, and M. Hamdi, Recensement Hivernal des Oiseaux d'Eau au Maroc en Janvier 1990. Porphyrio, 1989. 2(1/2): p. 65-88.

Jubete, F., Anuario Ornitológico de Palencia. Volumen 0. 1998.2001. 2005, Palencia: Asociación de Naturalistas Palentinos.

Leitao, A.H. and N. Cidraes-Vieira, Noticiário Ornitológico, 2005. Anuário Ornitológico (Portugal), 2007. 5: p. 35-73.

Leitao, A.H. and N. Cidraes-Vieira, Noticíario Ornitológico, 2006 e 2007. Anuário Ornitológico (Portugal), 2008. 6: p. 46-84.

Leitao, D., Contagens de Aves no Natal e no Ano Novo, 2004-2005. Anuário Ornitológico, 2006. 4: p. 65-72.

Lenglart, P.-Y., A. El Ghazi, and J. Franchimont, Chronique ornithologique du G.O.MAC. pour 1999 (2: Des Engoulevents aux Bruants). Porphyrio, 2001-2002. 13/14: p. 44-60.

Lorenzo, J.A., Anuario Ornitológico de Valladolid. 1997: SEO-Valladolid.

Luque, E. and J.V. Ortiz, Anuario Ornitológico de Castellón 2005, vol 3. 2007: http://www.internatura.org/aocs.

Maire, B., A. El Ghazi, and J. Franchimont, Chronique ornithologique du G.O.MAC. pour 1999 (1: Des Grebes aux Rapaces Nocturnes). Porphyrio, 2001-2002. 13/14: p. 20-43.

Marín Santos, J.C., Anuario Ornitológico de Toledo. Revisión Histórica / 2001. 2004, Toledo: Agrupación Naturalistica ESPARVEL.

Martín Barranco, F.J. and N. Sanchéz Pascual, Avifauna de Sierra Morena Oriental, Jaén. Boletín de Ecología, 1993. 41: p. 3-14.

Martínez-Vilalta, A., Descripción de la comunidad de limícolas invernante en el Delta del Ebro. Doñana - Acta vertebrata, 1985. 12(2).

Martínez-Vilalta, A., Anuari d'ornitologia de Catalunya. 1998. 2001, Barcelona: Group Català d'Anellament.

Martínez-Vilalta, A., Anuari d'ornitologia de Catalunya. 1999. 2002, Barcelona: Institut Català d'Ornitologia.

Mdarhri-Alaoui, E.K., Z.L. Arhzaf, and M. Thevenot, Chronique Ornithologique 1989/2 - Avril a Decembre. Porphyrio, 1990. 2(1/2): p. 65-88.

Melendro, J. and A. Rodriguez Valverde, Censo de Láridos y Pelecánidos invernantes en la costa de Pontevedra. Ardeola, 1977. 22: p. 75-83.

Miradas Cantabricas. http://miradascantabricas.blogspot.com/2008/11/breves-noticias-de-aves-en-el-cantbrico.html. 2009.

Molina, B. and J.A. Lorenzo, Noticiario Ornitológico, Junio 2004. Ardeola, 2004. 51(1): p. 245-54.

Molina, B. and J.A. Lorenzo, Noticiario Ornitológico. Ardeola, 2007. 54(2): p. 389-403.

Molina, B., J.A. Lorenzo, and C. López-Jurado, Noticiario Ornitológico. Ardeola, 2005B. 52(2): p. 423-435.

Molina, B., J.A. Lorenzo, and C. López-Jurado, Noticiario Ornitológico. Ardeola, 2008 b. 55(2): p. 289-307.

Molina, B., J.A. Lorenzo, and C. López-Jurado, Noticiario Ornitológico. Ardeola, 2008a. 55(1): p. 131-151.

Molina, B., R. Moreno-Opo, and J.A. Lorenzo, Noticiario Ornitológico, dic 2003. Ardeola, 2003. 50(2): p. 339-55.

Molina, B., R. Moreno-Opo, and J.A. Lorenzo, Noticiario Ornitológico, dic 2004. Ardeola, 2004. 51(2): p. 543-57.

Molina, B., R. Moreno-Opo, and J.A. Lorenzo, Noticiario Ornitológico. Ardeola, 2006a. 53(1): p. 191-211.

Molina, B., R. Moreno-Opo, and J.A. Lorenzo, Noticiario Ornitológico. Ardeola, 2007. 54(1): p. 169-183.

Molina, B., et al., Noticiario Ornitológico. Ardeola, 2006b. 53(2): p. 377-93.

Molina, B., et al., Noticiario Ornitológico. Ardeola, 2005a. 52(1): p. 207-224.

Molina, B., J. Prieta, and J.A. Lorenzo, Noticiario Ornitológico. Ardeola, 2009 A. 56(1): p. 151-172.

Moore, C.C., O estatuto da Petinha-de-garganta-ruiva Anthus cervinus em Portugal. Uma breve revisao. AIRO, 1990. 1(2): p. 5.

Moratalla, J.F. and J.P. Talavera, Censo invernal de Vaes en la dehesa se Santa Marta, La Roda (Albacete). La Calandria, 1990. 2: p. 8-9.

Múgica, J.H., ARTADI. Anuario Ornitológico de Bizkaia 1998-99. 2001, Bilbao: Sociedad Ornitológica LANIUS Ornitologi Elkartea.

Múgica, J.H. and I.G. Serna, ARTADI. Anuario Ornitológico de Bizkaia 2002-2003. 2008, Bilbao: Sociedad Ornitológica LANIUS Ornitologi Elkartea.

Munilla, I. and J. Guitián, Primeiro Anuario das Aves de Galicia, Anos 1992-1993. 1994.

Muselet, D., Les quartiers d'hivernage des Sternes pierregarins (Sterna hirundo) européennes. L'Oiseau et la Revue Française d'Ornithologie, 1982. 52(3): p. 219-235.

Navarrete Peréz, J., Noticiario Ornitológico. Revista Alcudón - SEO-Ceuta, 2005. 2: p. 26-38.

Navarro Medina, J.D. and J. Navarro Garcia, La Avifauna de los embalses de El Hondo (Alicante). Mediterranea - Series de estudios Biologicos - Universidad de Alicante, 1982. 6: p. 109-141.

Neves, R., Noticiário Ornitológico. AIRO, 1990. 1(2).

Neves, R., Noticiário Ornitológico. AIRO, 1991A. 2(1): p. 19-21.

Neves, R., Noticiário Ornitológico. AIRO, 1991B. 2(2): p. 54-56.

Neves, R., Noticiário Ornitológico. AIRO, 1992A. 3(1): p. 35-38.

Neves, R., Noticiário Ornitológico. AIRO, 1993 A 4(1): p. 38-40.

Neves, R., Noticiário Ornitológico. AIRO, 1993 B. 4(2): p. 78-80.

Padilla, E.A. and M. Garrido Sanchéz, Observaciones invernales de aves en la desembocadura del rio guadalhorce, Malaga. Años 1977-1981. Alytes, 1983. 1: p. 225-244.

Paracuellos, M., Dinamica anual de la comunidad de paseriformes en un saladar litoral del sudeste iberico. Doñana - Acta vertebrata, 1994. 21(2): p. 119-30.

Paracuellos, M., Dinámica anual de la comunidad de Paseriformes en carrizales costeros del suroeste ibérico-. Doñana - Acta vertebrata, 1996. 23(1): p. 33-44.

Paterson, A.M., Anuario Ornitológico de Malaga, 1994. 1995, Malaga: SEO-Malaga.

Paterson, A.M., Anuario Ornitológico de Malaga, 1995-97. 1998, Malaga: SEO-Malaga.

Pineau, J. and M. Giraud-Audine, Notes sur les oiseaux hivernant dans l'extrême Nord-Ouest du Maroc at sur leurs mouvements. Alauda, 1976. 44: p. 47-75.

Ponciano, J.A. and A.E. Garcia Rua, El Censo Español de Aves Acuaticas de enero de 1973. Boletin de la Estación Central de Ecología, num 4, 1973. 2: p. 11-39.

Pouteau, C., Chronique Ornithologique du G.O.MA.C. pour 1990. Porphyrio, 1991. 3(1/2): p. 49-110.

Pouteau, C., Chronique Ornithologique du G.O.MA.C. pour 1992. Porphyrio, 1993. 5(1/2): p. 60-154.

Pouteau, C., J. Franchimont, and A. Sayad, Chronique Ornithologique du G.O.MA.C. pour 1991. Porphyrio, 1992. 4(1/2): p. 39-117.

Prieta, J., Aves de Extremadura - Anuario ADENEX 1999-2000. 2003, Mérida: ADENEX.

Prieta, J. Noticiario Ornitológico Extremadura, Enero 2004. 2004a.

Prieta, J., Noticiario Ornitologico de Extremadura, Febrero 2004. 2004b.

Prieta, J. Noticiario Ornitológico Extremadura, Noviembre y DIciembre 2004. 2005a.

Prieta, J., Noticiario Ornitológico. Noviembre y diciembre 2004. 2005b.

Prieta, J. Noticiario Ornitológico Extremadura, Otoño 2005. 2005c.

Prieta, J., Noticiario Ornitológico de Extremadura, Otoño 2005. 2006.
Prieta, J. Noticiario Ornitológico Extremadura, Invierno 2005. 2006.
Prieta, J., Aves de Extremadura. Volumen 3. Anuario ADENEX 2001-2003. 2007, Mérida: ADENEX.
Prieta, J., V. Jesus, and J.M. Benitez, Aves de Extremadura. Vol 1. Anuario ADENEX 1998. 2000, Mérida: ADENEX.
Ramírez, J., Un posible caso de comportamiento sedentario de un Carricero Común Acrocephalus scirpaceus en una localidad del sur de España. Buttletí del Grup Catalá d'Anellament, 1998. 15: p. 51-53.
Ramírez, J., Noticiario Ornitológico del Estrecho de Gibraltar 2008. MIGRES - Revista de Ecología, 2009. 1: p. 175-190.
Ramos, R.S. and C.V. Rodríguez, III Anuario das Aves de Galicia, Ano 1995. 1996: GRUPO ERVA.
Reolid, J.M., Noticiario Ornitológico. La Calandria, 1998. 6: p. 20-25.
Romay Cousido, C.D., IX Anuario das Aves de Galicia, 2001. 2004, Santiago de Compostela: Sociedade Galega de Ornitoloxía.
Rubio Garcia, J.C., Estudio de la comunidad de limicolos de las marismas del Odiel (Huelva). Oxyura, 1986. 3(1): p. 97-132.
Rui, R. and L.T. Costa, Contagens de aves aquáticas em Portugal Janeiro de 1993. AIRO, 1993. 4(2): p. 57-67.
Ruiz, A.G., Estudio y sitación de la pobalción de Cigueña Blanca (Ciconia ciconia) en Jaén según los últimos censos provinciales 1994-1996. Boletín de Ecología, 1997. 46: p. 3-15.
Salaverri, L.J. and I. Munilla, Segundo Anuario das Aves de Galicia, Ano 1994. 1995.
Salaverri, L.J. and J. Taboada, XI Anuario das Aves de Galicia, 2003. 2007, Santiago de Compostela: Sociedade Galega de Ornitoloxía.
Sales, S., Anuari d'Ornitologia de Catalunya. 2002-2005. 2006, Barcelona: Institut Català d'Ornitologia.
Salvadores, R. and C. Vidal, VII Anuario das Aves de Galicia 1999. 2002, Santiago de Compostela: Sociedade Galega de Ornitoloxía.
Sánchez Cobo, M., Anuario Ornitológico de Cantabria. Años 2001 y 2002. 2003.
Sánchez Moreno, A., Resultados de los censos de aves acuáticas invernantes en el sur-oeste de España. Inviernos de 1975-76 y de 1976-77. Doñana - Acta vertebrata, 1979. 6(1): p. 67-75.
Sánchez Sanz, J.M., Rocín - Anuario Ornitológico de Aragón 1991-1992. 1994, Zaragoza: SEO-Aragón.
Sánchez Sanz, J.M., Rocín - Anuario Ornitológico de Aragón 1993-1994. 1996, Zaragoza: SEO-Aragón.
Sánchez Sanz, J.M., Rocín - Anuario Ornitológico de Aragón 1995-1996. 1997, Zaragoza: SEO-Aragón.
Sánchez Sanz, J.M., Rocín - Anuario Ornitológico de Aragón 1997-1998. 1999, Zaragoza: SEO-Aragón.
Sanchez-Lafuente, A.M. and J. Muñoz-Cobo, Avifauna de las zonas humedas del alto Guadalquivir (Jaen). Oxyura, 1989. 5(1): p. 45-59.
Sarmiento, L.F. and A.J. Ramos-Sánchez, Noticiario Ornitológico. La Matruca, 1998. 10: p. 8-11.
Schollaert, V., A. El Ghazi, and J. Franchimont, Chronique ornithologique du G.O.MAC. pour 1998. Porphyrio, 2000. 12(1/2): p. 16-29.
Schollaert, V. and J. Franchimont, Chronique ornithologique du G.O.MAC. pour 1994. Porphyrio, 1995. 7(1): p. 99-146.
Schollaert, V. and J. Franchimont, Chronique ornithologique du G.O.MAC. pour 1995. Porphyrio, 1996. 8(1/2): p. 94-150.
Schollaert, V., et al., Chronique ornithologique du G.O.MAC. pour 1993. Porphyrio, 1994. 6(2): p. 1-108.
SEO-Alicante, Las Aves en Alicante. Anuario Ornitológico 1999. 2001, Alicante.
SEO-Alicante, Las aves en Alicante. Anuario Ornitológico 2000. 2002, Alicante.
SEO-Alicante, Las Aves en Alicante. Anuario Ornitológico 2001-2002-2003. 2006, Alicante.
SEO-Ceuta and Grupo Anillamiento "Chagra", Revista Alcudón Nº1. 2003, Ceuta.
SEO-Jaén, Noticiario. Apuntes a la Historia Natural de Jaén. El Alcaraván. Revista de Historia natural de la provincia de Jaén., 2009. 2: p. 51-55.
Sociedad Albacetense de Ornitología, Anuario ornitológico de Albacete 1997 y 1998. 2001, Albacete: SAO. 241.
Sociedade Galega de Ornitoloxia. Noticiario Ornitolóxico http://www.sgosgo.org/noticiario_fecha.asp. 2009 23 nov 2009].
Societat Valenciana d'Ornitologia, Aves de la Comunidad Valenciana, 1998. 1999, Valencia.

Societat Valenciana d'Ornitologia, Aves de la Comunidad Valenciana, 1999. 2003, Valencia.

Soler, J.C., Fenología reproductiva, status y distribución del avetorillo común Ixobrychus minutus (Linnaeus 1766), en la región de Murcia. Oxyura, 1997. 9(1): p. 53-83.

Suarez, M., et al., Registres Ornitológics. Anuari Ornitológico de les Baleares, 2003, 2004. 18: p. 107-211.

Suarez, M., O. Martinez, and D. Garcia, Recompte hivernal d'aus aquátiques i limicoles a les baleares, gener 2003-2004. Anuari Ornitológico de les Baleares, 2003, 2004. 18: p. 81-92.

Talavera, P. and J. Ortega, A.N.S.E., Circular informativa asociación de naturalistas del sureste 1975-76. 1977, Alicante-Murcia-Almeria.

Tato Cumming, J.J., Notas invernales de la zona costera del sur-este de España. Ardeola, 1960. 6(2): p. 362-63.

Telleria, J.L., La migración de las aves en el estrecho de Gibraltar. Vol II: Aves no planeadoras. 1981, Madrid: Universidad Complutense.

The Gibraltar Ornithological & Natural History Society, Alectoris. The biannual report of the Gibraltar Ornithological Society 1977, n.1. Alectoris. 1978, Gibraltar.

The Gibraltar Ornithological & Natural History Society, Alectoris. The biannual report of the Gibraltar Ornithological Society 1978, n.2. 1979, Gibraltar.

The Gibraltar Ornithological & Natural History Society, Alectoris. The biannual report of the Gibraltar Ornithological Society 1979, n.3. 1981, Gibraltar.

The Gibraltar Ornithological & Natural History Society, Alectoris. The biannual report of the Gibraltar Ornithological Society 1980, n.4. 1982, Gibraltar.

The Gibraltar Ornithological & Natural History Society, Alectoris. The biannual report of the Gibraltar Ornithological Society 1981-82, n.5. 1983, Gibraltar.

The Gibraltar Ornithological & Natural History Society, Alectoris (n.6). The birds of the Strait of Gibraltar Bird Observatory, 1986. 1987, Gibraltar.

The Gibraltar Ornithological & Natural History Society, The strait of Gibraltar Bird Observatory monthly report - February 1987. 1987a, Gibraltar: The Gibraltar Museum.

The Gibraltar Ornithological & Natural History Society, The strait of Gibraltar Bird Observatory monthly report - November 1987. 1987b, Gibraltar: The Gibraltar Museum.

The Gibraltar Ornithological & Natural History Society, The strait of Gibraltar Bird Observatory monthly report - January 1988. 1988a, Gibraltar: The Gibraltar Museum.

The Gibraltar Ornithological & Natural History Society, The strait of Gibraltar Bird Observatory monthly report - December 1987. 1988b, Gibraltar: The Gibraltar Museum.

The Gibraltar Ornithological & Natural History Society, The strait of Gibraltar Bird Observatory monthly report - February 1988. 1988c, Gibraltar: The Gibraltar Museum.

The Gibraltar Ornithological & Natural History Society, The strait of Gibraltar Bird Observatory monthly report - November 1988. 1988d, Gibraltar: The Gibraltar Museum.

The Gibraltar Ornithological & Natural History Society, The strait of Gibraltar Bird Observatory monthly report - December 1988. 1989a, Gibraltar: The Gibraltar Museum.

The Gibraltar Ornithological & Natural History Society, The strait of Gibraltar Bird Observatory monthly report - January/March 1989. 1989b, Gibraltar: The Gibraltar Museum.

The Gibraltar Ornithological & Natural History Society, Alectoris. The annual report of the Starit of Gibraltar Bird Obseravtory, 1987, number 7. 1990, Gibraltar.

The Gibraltar Ornithological & Natural History Society, The strait of Gibraltar Bird Observatory monthly report - October/November/December 1989. 1990a, Gibraltar: The Gibraltar Museum.

The Gibraltar Ornithological & Natural History Society, The strait of Gibraltar Bird Observatory monthly report - January/February/March 1990. 1990b, Gibraltar: The Gibraltar Museum.

The Gibraltar Ornithological & Natural History Society, The strait of Gibraltar Bird Observatory monthly report - Jan/Feb/Mar 1993. 1993, Gibraltar: Gibraltar Natural History Field Centre.

The Gibraltar Ornithological & Natural History Society, Alectoris. The annual report of the Strait of Gibraltar Bird Observatory, 1988, number 8. 1993.

The Gibraltar Ornithological & Natural History Society, The strait of Gibraltar Bird Observatory monthly report - Oct/Nov/Dec 1993. 1994, Gibraltar: Gibraltar Natural History Field Centre.

The Gibraltar Ornithological & Natural History Society, The strait of Gibraltar Bird Observatory monthly report - 1995 - Part one - January to June. 1995, Gibraltar: Gibraltar Natural History Field Centre.

The Gibraltar Ornithological & Natural History Society, Alectoris, The annual report of the strait of Gibraltar bird Observatory, 1989 y 1990, number 9. 1995, Gibraltar.

The Gibraltar Ornithological & Natural History Society, Gibraltar Bird Report 2001. 2003, Gibraltar.

The Gibraltar Ornithological & Natural History Society, Gibraltar Bird Report 2002. 2004, Gibraltar.

The Gibraltar Ornithological & Natural History Society, Gibraltar Bird Report 2003. 2005, Gibraltar.

The Gibraltar Ornithological & Natural History Society, Gibraltar Bird Report 2004. 2005, Gibraltar.

The Gibraltar Ornithological & Natural History Society, Gibraltar Bird Report 2005. 2006, Gibraltar.

The Gibraltar Ornithological & Natural History Society, Gibraltar Bird Report 2006. 2007, Gibraltar.

The Gibraltar Ornithological & Natural HIstroy Society, Gibraltar Bird Report 2007. 2008, Gibraltar: GONHS.

Thévenot, M., Compte-rendu d'activite de la station de baguage du Maroc. Bulletin de la Société des Sciences Naturelles et Physiques du Maroc. 3º et 4º trimestres 1972, 1972. 52: p. 243-288.

Thévenot, M., Compte-rendu d'activite de la station de baguage du Maroc. Année 1972. Bulletin de la Société des Sciences Naturelles et Physiques du Maroc. 1º et 2º trimestres 1974, 1974. 54: p. 81-103.

Thévenot, M. and R. Magnin, Quelques observations ornithologiques hivernales dans le nord du Maroc (hiver 1969-70). Bulletin de la Société des Sciences Naturelles et Physiques du Maroc, 1971. 51: p. 235-246.

Thevenot, M. and P. Thouy, Nidification ou hivernage d'espèces peu connues ou nouvelles pour le Maroc. Alauda, 1974. XLII(1): p. 51-56.

Thévenot, M., R. Vernon, and P. Bergier, The birds of Morocco. BOU Checklist series. Vol. BOU Checklist series nº 20. 2003: The Natural History Museum: Tring, Herts UK.

Tirado, M. and V.C. Esteller, Anuario Ornitológico de Castellón, 2006. Vol. 4. 2008, Castellón: http://www.internatura.org/aocs.

Torralvo, C., Anuario Ornitológico de Ciudad Real. 2002-2003. 2004, Ciudad Real: SEO - Ciudad Real.

Torralvo, C.A., Anuario Ornitológico de Ciudad Real, 1995-2001. 2002, Ciudad Real: SEO-Ciudad Real.

Vidal, C. and L.J. Salaverri, VIII Anuario das Aves de Galicia, 2000. 2003, Santiago de Compostela: Sociedade Galega de Ornitoloxía.

VV.AA., Notas Ornitologicas Breves, 1973. Ardeola, 1973. 19(1): p. 7-40.

VV.AA., Notas Ornitológicas breves, 1977. Ardeola, 1977. 22(1): p. 103-49.

VV.AA., Notas Ornitológicas Breves, 1978. Ardeola, 1978. 24(1): p. 253-64.

VV.AA., Contagens de Aves no Natal e no Ano Novo, 2005-2006. Anúario Ornitologico, 2007. 5: p. 144-151.

VV.AA., Contagens de Aves no Natal e no Ano Novo, 2006-2007. Anúario Ornitologico, 2008. 6: p. 95-102.

Table S2, Chapter II

Specific values of the 21 ecological and phenological variables for the 69 species condiered in the phylogentically-corrected GEE models. Because of the dimensions (69 records X 21 columns), table is given in part both for records and for columns.

PART I/III

	Species	European Population [log(nºpairs)]	Northermost breeding latitude (Lat º)	Southermost breeding latitude (Lat º)	Breeding range extension (Lat º)	Mean breeding latitude (Lat º)	Northermost wintering latitude (Lat º)	Southermost wintering latitude (Lat º)	Wintering range extension (Lat º)	Mean wintering latitude (Lat º)	...
1	Acrocephalus arundinaceus	4.79	61.37	36.01	25.36	48.69	17.45	-30.25	47.70	-6.40	
2	Acrocephalus paludicola	4.08	56.56	47.00	9.56	51.78	16.39	14.04	2.35	15.22	
3	Acrocephalus schoenobaenus	5.69	70.39	40.00	30.39	55.20	18.31	-33.39	51.70	-7.54	
4	Acrocephalus scirpaceus	5.73	64.24	36.01	28.23	50.13	18.10	-13.55	31.65	2.28	
5	Anas querquedula	3.66	65.44	38.37	27.07	51.91	15.46	-1.06	16.52	7.20	
6	Anthus campestris	5.76	59.33	35.00	24.33	47.17	20.00	2.52	17.48	11.26	
7	Anthus trivialis	6.09	70.38	39.07	31.31	54.73	9.09	-23.18	32.27	-7.05	
8	Apus apus	6.62	69.55	35.00	34.55	52.28	-2.03	-24.02	21.99	-13.03	
9	Ardea purpurea	3.84	53.00	30.00	23.00	41.50	26.06	-34.45	60.51	-4.20	
10	Ardeola ralloides	3.23	49.40	31.05	18.35	40.23	18.27	-33.43	51.70	-7.58	
11	Caprimulgus europaeus	5.35	62.12	35.00	27.12	48.56	12.27	-34.45	46.72	-11.09	
12	Caprimulgus ruficollis	4.82	42.27	35.00	7.27	38.64	17.07	15.24	1.83	16.16	
13	Charadrius dubius	4.38	66.50	32.23	34.27	49.37	15.27	-3.20	18.47	6.04	
14	Chlidonias hybrida	4.06	47.17	36.49	10.68	41.83	19.48	-34.45	53.93	-7.49	
15	Chlidonias niger	3.39	61.57	43.34	18.23	52.46	17.38	-24.12	41.50	-3.37	
16	Ciconia nigra	3.05	60.00	39.47	20.53	49.74	-8.43	-34.45	26.02	-21.44	
17	Circaetus gallicus	3.77	59.52	29.19	30.33	44.36	16.53	10.19	6.34	13.36	
18	Circus pygargus	4.08	61.05	32.33	28.72	46.69	17.52	-32.53	50.05	-7.51	
19	Clamator glandarius	4.79	44.38	36.02	8.36	40.20	16.20	-16.27	32.47	-0.04	
20	Coracias garrulus	3.47	59.36	35.00	24.36	47.18	3.04	-33.50	36.54	-15.23	
21	Crex crex	3.67	66.05	42.11	23.94	54.08	1.45	-30.37	31.82	-14.46	
22	Cuculus canorus	5.92	70.17	35.00	35.17	52.59	-1.47	-33.53	32.06	-17.50	
23	Delichon urbica	6.78	70.08	30.00	40.08	50.04	17.41	-34.45	51.86	-8.52	
24	Emberiza hortulana	5.41	67.58	40.08	27.50	53.83	22.48	9.43	13.05	15.96	
25	Erythropygia galactotes	4.15	40.40	25.57	14.83	32.99	21.07	14.44	6.63	17.76	
26	Falco eleonorae	3.03	42.44	29.24	13.20	35.84	-12.00	-17.00	5.00	-14.50	
27	Falco naumanni	4.30	54.18	35.00	19.18	44.59	22.00	-34.45	56.45	-6.23	
28	Falco subbuteo	4.28	66.12	31.06	35.06	48.59	-7.44	-31.50	24.06	-19.47	
29	Ficedula hypoleuca	5.77	70.45	38.48	31.97	54.47	9.44	4.22	5.22	6.83	
30	Glareola pratincola	3.73	47.05	30.00	17.05	38.53	20.00	-31.57	51.57	-5.79	
31	Hieraaetus pennatus	3.62	56.28	30.21	26.07	43.25	14.46	-34.45	48.91	-10.00	
32	Hippolais polyglotta	6.30	50.41	35.00	15.41	42.71	12.48	4.09	8.39	8.29	
33	Hirundo daurica	5.06	45.00	30.00	15.00	37.50	16.11	-8.41	24.52	3.85	
...	continnue										

	Species	European Population [log(nºpairs)]	Northermost breeding latitude (Lat º)	Southermost breeding latitude (Lat º)	Breeding range extension (Lat º)	Mean breeding latitude (Lat º)	Northermost wintering latitude (Lat º)	Southermost wintering latitude (Lat º)	Wintering range extension (Lat º)	Mean wintering latitude (Lat º)
	Continue from the previous page									...
34	Hirundo rustica	6.88	70.08	35.00	35.08	52.54	13.14	-34.45	47.59	-10.66
35	Ixobrychus minutus	3.68	59.50	30.00	29.50	44.75	14.43	-33.47	47.90	-9.52
36	Lanius collurio	5.57	65.55	37.54	28.01	51.55	-0.53	-33.22	32.69	-16.88
37	Lanius senator	5.85	52.53	31.10	21.43	41.82	22.29	4.23	18.06	13.26
38	Locustella luscinioides	4.25	58.40	37.00	21.40	47.70	16.11	9.15	6.96	12.63
39	Locustella naevia	5.22	65.00	43.07	21.93	54.04	20.00	9.39	10.61	14.70
40	Luscinia megarhynchos	6.53	54.42	35.00	19.42	44.71	20.45	-4.30	24.75	8.08
41	Merops apiaster	5.31	57.53	35.00	22.53	46.27	17.15	-34.45	51.60	-8.65
42	Milvus migrans	4.57	66.06	28.20	37.86	47.13	21.55	-33.43	54.98	-5.94
43	Motacilla flava	6.08	70.33	36.01	34.32	53.17	20.00	-34.45	54.45	-7.23
44	Muscicapa striata	6.30	70.45	35.00	35.45	52.73	7.59	-34.45	42.04	-13.43
45	Neophron percnopterus	3.20	47.47	28.00	19.47	37.74	19.30	-2.07	21.37	8.62
46	Numenius phaeopus	2.72	70.04	56.12	13.92	63.08	20.00	-34.45	54.45	-7.23
47	Nycticorax nycticorax	4.33	52.14	30.00	22.14	41.07	22.39	-34.42	56.81	-6.02
48	Oenanthe oenanthe	5.79	71.08	36.01	35.07	53.55	21.01	-11.06	32.07	4.98
49	Oriolus oriolus	5.85	63.59	36.01	27.58	49.80	6.36	-34.45	40.81	-14.05
50	Otus scops	4.71	58.38	35.00	23.38	46.69	17.52	6.26	11.26	11.89
51	Pandion haliaetus	2.74	69.38	45.00	24.38	57.19	20.00	-34.45	54.45	-7.23
52	Pernis apivorus	4.32	67.11	38.43	28.68	52.77	9.03	-29.41	38.44	-10.19
53	Phoenicurus phoenicurus	5.74	70.35	36.01	34.34	53.18	21.07	0.12	20.95	10.60
54	Phylloscopus bonelli	6.36	49.07	35.00	14.07	42.04	17.06	13.27	3.79	15.17
55	Phylloscopus sibilatrix	5.41	68.12	40.00	28.12	54.06	7.59	-6.56	14.15	0.52
56	Phylloscopus trochilus	7.47	71.08	45.00	26.08	58.04	14.55	-34.45	49.00	-9.95
57	Riparia riparia	5.87	70.32	36.01	34.31	53.17	20.00	-29.02	49.02	-4.51
58	Saxicola rubetra	5.20	70.00	41.25	28.75	55.63	20.00	-17.27	37.27	1.37
59	Sterna albifrons	4.20	58.38	35.00	23.38	46.69	20.00	-34.45	54.45	-7.23
60	Sterna hirundo	4.79	71.05	35.00	36.05	53.03	18.28	-34.45	52.73	-8.09
61	Sterna nilotica	3.61	56.48	35.00	21.48	45.74	18.28	-2.52	20.80	7.88
62	Streptopelia turtur	6.23	63.54	27.53	36.01	45.54	19.46	11.41	8.05	15.44
63	Sylvia borin	6.86	70.30	40.00	30.30	55.15	11.59	-31.45	43.04	-9.93
64	Sylvia cantillans	6.27	45.47	35.00	10.47	40.24	22.06	13.04	9.02	17.55
65	Sylvia communis	6.54	68.14	36.01	32.13	52.08	18.48	-5.51	23.99	6.49
66	Sylvia hortensis	5.29	45.43	35.00	10.43	40.22	18.09	13.01	5.08	15.55
67	Tachymarptis melba	4.34	47.05	35.00	12.05	41.03	15.40	-34.45	49.85	-9.53
68	Tringa glareola	5.53	71.05	51.22	19.83	61.14	17.10	-34.45	51.55	-8.68
69	Tringa nebularia	3.05	70.06	50.00	20.06	60.03	20.00	-34.45	54.45	-7.23

PART II/III

	Species ...	Migration distance (Lat °)	Start of the breeding season (weeks)	End of the breeding season (weeks)	Mean of the breeding season (week)	Start of spring migration (weeks)	End of spring migration (weeks)	Mean of spring migration (weeks)	Start of fall migration (weeks)	End of fall migration (weeks) ...
1	Acrocephalus arundinaceus	55.09	21.00	29.00	25.00	12.00	18.00	15.00	30.00	40.00
2	Acrocephalus paludicola	36.57	19.00	30.00	24.50	10.00	18.00	14.00	27.00	38.00
3	Acrocephalus schoenobaenus	62.74	18.00	30.00	24.00	9.00	20.00	14.50	29.00	39.00
4	Acrocephalus scirpaceus	47.85	21.00	32.00	26.50	11.00	20.00	15.50	29.00	40.00
5	Anas querquedula	44.71	16.00	29.00	22.50	9.00	16.00	12.50	30.00	39.00
6	Anthus campestris	35.91	19.00	23.00	21.00	15.00	18.00	16.50	33.00	37.00
7	Anthus trivialis	61.77	16.00	29.00	22.50	9.00	20.00	14.50	32.00	36.00
8	Apus apus	65.30	20.00	32.00	26.00	12.00	18.00	15.00	29.00	38.00
9	Ardea purpurea	45.70	19.00	29.00	24.00	9.00	16.00	12.50	31.00	40.00
10	Ardeola ralloides	47.81	18.00	30.00	24.00	9.00	17.00	13.00	31.00	40.00
11	Caprimulgus europaeus	59.65	21.00	32.00	26.50	12.00	18.00	15.00	32.00	41.00
12	Caprimulgus ruficollis	22.48	17.00	25.00	21.00	11.00	17.00	14.00	33.00	41.00
13	Charadrius dubius	43.33	15.00	34.00	24.50	10.00	16.00	13.00	28.00	40.00
14	Chlidonias hybrida	49.32	22.00	27.00	24.50	14.00	20.00	17.00	30.00	37.00
15	Chlidonias niger	55.83	20.00	27.00	23.50	14.00	18.00	16.00	30.00	37.00
16	Ciconia nigra	71.18	16.00	29.00	22.50	11.00	16.00	13.50	34.00	42.00
17	Circaetus gallicus	31.00	18.00	37.00	27.50	9.00	14.00	11.50	33.00	38.00
18	Circus pygargus	54.20	20.00	24.00	22.00	11.00	17.00	14.00	31.00	38.00
19	Clamator glandarius	40.24	13.00	24.00	18.50	8.00	13.00	10.50	26.00	36.00
20	Coracias garrulus	62.41	22.00	30.00	26.00	13.00	20.00	16.50	31.00	40.00
21	Crex crex	68.54	18.00	32.00	25.00	11.00	18.00	14.50	33.00	44.00
22	Cuculus canorus	70.09	17.00	27.00	22.00	12.00	17.00	14.50	29.00	40.00
23	Delichon urbica	58.56	16.00	33.00	24.50	8.00	19.00	13.50	33.00	42.00
24	Emberiza hortulana	37.88	21.00	23.00	22.00	15.00	19.00	17.00	33.00	38.00
25	Erythropygia galactotes	15.23	19.00	22.00	20.50	17.00	21.00	19.00	33.00	37.00
26	Falco eleonorae	50.34	28.00	36.00	32.00	15.00	21.00	18.00	37.00	42.00
27	Falco naumanni	50.82	17.00	24.00	20.50	8.00	14.00	11.00	32.00	40.00
28	Falco subbuteo	68.06	21.00	31.00	26.00	13.00	20.00	16.50	35.00	42.00
29	Ficedula hypoleuca	47.64	15.00	24.00	19.50	9.00	17.00	13.00	27.00	37.00
30	Glareola pratincola	44.31	18.00	30.00	24.00	12.00	16.00	14.00	32.00	39.00
31	Hieraaetus pennatus	53.24	18.00	29.00	23.50	10.00	16.00	13.00	35.00	39.00
32	Hippolais polyglotta	34.42	18.00	28.00	23.00	11.00	20.00	15.50	29.00	40.00
33	Hirundo daurica	33.65	16.00	33.00	24.50	7.00	16.00	11.50	33.00	39.00
34	Hirundo rustica	63.20	19.00	32.00	25.50	7.00	18.00	12.50	31.00	44.00
35	Ixobrychus minutus	54.27	20.00	30.00	25.00	13.00	17.00	15.00	32.00	42.00
36	Lanius collurio	68.42	18.00	22.00	20.00	15.00	21.00	18.00	31.00	34.00
37	Lanius senator	28.56	17.00	27.00	22.00	15.00	19.00	17.00	32.00	34.00
38	Locustella luscinioides	35.07	18.00	29.00	23.50	9.00	17.00	13.00	32.00	39.00
...	continue									

	Species ...	Migration distance (Lat °)	Start of the breeding season (weeks)	End of the breeding season (weeks)	Mean of the breeding season (week)	Start of spring migration (weeks)	End of spring migration (weeks)	Mean of spring migration (weeks)	Start of fall migration (weeks)	End of fall migration (weeks) ...
	Continue from prevous page									
39	Locustella naevia	39.34	16.00	30.00	23.00	10.00	18.00	14.00	29.00	39.00
40	Luscinia megarhynchos	36.64	18.00	21.00	19.50	13.00	17.00	15.00	29.00	33.00
41	Merops apiaster	54.92	19.00	28.00	23.50	11.00	18.00	14.50	32.00	39.00
42	Milvus migrans	53.07	14.00	29.00	21.50	8.00	16.00	12.00	29.00	38.00
43	Motacilla flava	60.40	16.00	21.00	18.50	10.00	18.00	14.00	29.00	41.00
44	Muscicapa striata	66.16	20.00	30.00	25.00	13.00	21.00	17.00	30.00	41.00
45	Neophron percnopterus	29.12	13.00	32.00	22.50	10.00	18.00	14.00	30.00	35.00
46	Numenius phaeopus	70.31	20.00	31.00	25.50	12.00	18.00	15.00	30.00	38.00
47	Nycticorax nycticorax	47.09	17.00	31.00	24.00	9.00	14.00	11.50	33.00	42.00
48	Oenanthe oenanthe	48.57	16.00	28.00	22.00	8.00	17.00	12.50	32.00	39.00
49	Oriolus oriolus	63.85	19.00	25.00	22.00	13.00	18.00	15.50	29.00	34.00
50	Otus scops	34.80	16.00	28.00	22.00	11.00	16.00	13.50	31.00	37.00
51	Pandion haliaetus	64.42	16.00	28.00	22.00	11.00	16.00	13.50	33.00	40.00
52	Pernis apivorus	62.96	21.00	33.00	27.00	15.00	21.00	18.00	32.00	40.00
53	Phoenicurus phoenicurus	42.59	18.00	22.00	20.00	12.00	17.00	14.50	31.00	40.00
54	Phylloscopus bonelli	26.87	18.00	25.00	21.50	8.00	18.00	13.00	27.00	34.00
55	Phylloscopus sibilatrix	53.55	19.00	22.00	20.50	13.00	18.00	15.50	29.00	42.00
56	Phylloscopus trochilus	67.99	17.00	26.00	21.50	11.00	18.00	14.50	29.00	41.00
57	Riparia riparia	57.68	18.00	27.00	22.50	11.00	17.00	14.00	30.00	40.00
58	Saxicola rubetra	54.26	18.00	26.00	22.00	11.00	17.00	14.00	32.00	41.00
59	Sterna albifrons	53.92	20.00	30.00	25.00	13.00	18.00	15.50	31.00	37.00
60	Sterna hirundo	61.11	19.00	32.00	25.50	12.00	17.00	14.50	31.00	37.00
61	Sterna nilotica	37.86	18.00	29.00	23.50	13.00	17.00	15.00	27.00	37.00
62	Streptopelia turtur	30.10	20.00	34.00	27.00	9.00	16.00	12.50	33.00	41.00
63	Sylvia borin	65.08	18.00	28.00	23.00	11.00	21.00	16.00	29.00	42.00
64	Sylvia cantillans	22.69	13.00	24.00	18.50	10.00	16.00	13.00	33.00	40.00
65	Sylvia communis	45.59	18.00	29.00	23.50	13.00	20.00	16.50	29.00	39.00
66	Sylvia hortensis	24.67	16.00	21.00	18.50	8.00	18.00	13.00	28.00	36.00
67	Tachymarptis melba	50.55	19.00	26.00	22.50	12.00	20.00	16.00	32.00	39.00
68	Tringa glareola	69.81	19.00	29.00	24.00	13.00	17.00	15.00	22.00	37.00
69	Tringa nebularia	67.26	17.00	28.00	22.50	13.00	16.00	14.50	26.00	36.00

PART III/III

	Species ...	Mean of fall migration (weeks)	Length of the period spent north of the Sahara (weeks)	Body mass [log(g)]
1	Acrocephalus arundinaceus	35.00	20.00	1.50
2	Acrocephalus paludicola	32.50	18.50	1.07
3	Acrocephalus schoenobaenus	34.00	19.50	1.05
4	Acrocephalus scirpaceus	34.50	19.00	1.07
5	Anas querquedula	34.50	22.00	2.58
6	Anthus campestris	35.00	18.50	1.40
7	Anthus trivialis	34.00	19.50	1.35
8	Apus apus	33.50	18.50	1.62
9	Ardea purpurea	35.50	23.00	2.94
10	Ardeola ralloides	35.50	22.50	2.46
11	Caprimulgus europaeus	36.50	21.50	1.89
12	Caprimulgus ruficollis	37.00	23.00	1.84
13	Charadrius dubius	34.00	21.00	1.59
14	Chlidonias hybrida	33.50	16.50	1.94
15	Chlidonias niger	33.50	17.50	1.82
16	Ciconia nigra	38.00	24.50	3.48
17	Circaetus gallicus	35.50	24.00	3.23
18	Circus pygargus	34.50	20.50	2.50
19	Clamator glandarius	31.00	20.50	2.18
20	Coracias garrulus	35.50	19.00	2.13
21	Crex crex	38.50	24.00	2.17
22	Cuculus canorus	34.50	20.00	2.06
23	Delichon urbica	37.50	24.00	1.27
24	Emberiza hortulana	35.50	18.50	1.39
25	Erythropygia galactotes	35.00	16.00	1.36
26	Falco eleonorae	39.50	21.50	2.57
27	Falco naumanni	36.00	25.00	2.18
28	Falco subbuteo	38.50	22.00	2.32
29	Ficedula hypoleuca	32.00	19.00	1.11
30	Glareola pratincola	35.50	21.50	1.91
31	Hieraaetus pennatus	37.00	24.00	2.93
32	Hippolais polyglotta	34.50	19.00	1.05
33	Hirundo daurica	36.00	24.50	1.35
34	Hirundo rustica	37.50	25.00	1.28
35	Ixobrychus minutus	37.00	22.00	2.17
36	Lanius collurio	32.50	14.50	1.48
37	Lanius senator	33.00	16.00	1.60
38	Locustella luscinioides	35.50	22.50	1.21
39	Locustella naevia	34.00	20.00	1.12
40	Luscinia megarhynchos	31.00	16.00	1.30
41	Merops apiaster	35.50	21.00	1.76
42	Milvus migrans	33.50	21.50	2.92
43	Motacilla flava	35.00	21.00	1.26
44	Muscicapa striata	35.50	18.50	1.16
45	Neophron percnopterus	32.50	18.50	3.28
46	Numenius phaeopus	34.00	19.00	2.62
47	Nycticorax nycticorax	37.50	26.00	2.80
48	Oenanthe oenanthe	35.50	23.00	1.31
49	Oriolus oriolus	31.50	16.00	1.84
50	Otus scops	34.00	20.50	1.94
51	Pandion haliaetus	36.50	23.00	3.18
52	Pernis apivorus	36.00	18.00	2.88
53	Phoenicurus phoenicurus	35.50	21.00	1.21
54	Phylloscopus bonelli	30.50	17.50	0.93
55	Phylloscopus sibilatrix	35.50	20.00	0.99
56	Phylloscopus trochilus	35.00	20.50	0.92
57	Riparia riparia	35.00	21.00	1.12
58	Saxicola rubetra	36.50	22.50	1.22
59	Sterna albifrons	34.00	18.50	1.72
60	Sterna hirundo	34.00	19.50	2.10
61	Sterna nilotica	32.00	17.00	2.37
62	Streptopelia turtur	37.00	24.50	2.17
63	Sylvia borin	35.50	19.50	1.28
64	Sylvia cantillans	36.50	23.50	1.04
65	Sylvia communis	34.00	17.50	1.20
66	Sylvia hortensis	32.00	19.00	1.32
67	Tachymarptis melba	35.50	19.50	1.99
68	Tringa glareola	29.50	14.50	1.79
69	Tringa nebularia	31.00	16.50	2.26

Table S1, Chapter III

List of the 77 trans-Saharan species for which wintering episodes in Iberia and Morocco between 1969 and 2006 were collected. For each species the considered mean breeding latitude and phenological variables are given.

	Species	Mean breeding lat. (decimal degrees)	Breeding lat. Group (see Figure 2)	Wintering window	Autumn migr. end	Mean aut. migr. (+- 2wks)	Spring migr. end	Mean spring migr. (+- 2wks)
1	Acrocephalus arundinaceus	48.7	F	DEC - FEB	IV OCT	III SEP	II MAY	III APR
2	Acrocephalus paludicola	51.8	G	DEC - FEB	II OCT	I SEP	II MAY	II APR
3	Acrocephalus schoenobaenus	55.2	H	NOV - FEB	III OCT	II SEP	IV MAY	III APR
4	Acrocephalus scirpaceus	50.1	F	DEC - FEB	IV OCT	III SEP	IV MAY	IV APR
5	Anas querquedula	51.9	G	DEC - JAN	III OCT	III SEP	IV APR	I APR
6	Anthus campestris	47.2	E	NOV - FEB	I OCT	III SEP	II MAY	I MAY
7	Anthus cervinus	68.6	M	DEC - FEB	I NOV	I OCT	IV MAY	I APR
8	Anthus trivialis	54.7	H	DEC - FEB	IV SEP	II SEP	IV MAY	III APR
9	Apus apus	52.3	G	DEC - JAN	II OCT	II SEP	II MAY	III APR
10	Apus melba	41	B	DEC - JAN	III OCT	IV SEP	IV MAY	IV APR
11	Apus pallidus	40*	B	DEC - JAN	I OCT	I OCT	I APR	IV FEB
12	Ardea purpurea	41.5	C	DEC - FEB	IV OCT	IV SEP	IV APR	I APR
13	Ardeola ralloides	40.2	B	NOV - FEB	IV OCT	IV SEP	I MAY	I APR
14	Calandrella brachydactyla	41.3	C	DEC - JAN	II OCT*	III SEP*	IV MAY**	I MAR
15	Caprimulgus europaeus	48.6	E	DEC - JAN	I NOV	I OCT	II MAY	III APR
16	Caprimulgus ruficollis	38.6	B	DEC - JAN	I NOV	I OCT	I MAY	II APR
17	Cercotrichas galactotes	37.5	A	NOV - JAN	I OCT	III SEP	I JUN*	III MAY
18	Charadrius dubius	49.4	F	NOV - FEB	IV OCT	II SEP	IV APR	I APR
19	Chlidonias hybrida	41.8	C	DEC - FEB	I OCT	II SEP	IV MAY	I MAY
20	Chlidonias leucopterus	49.9	F	DEC - FEB	I OCT	II SEP	IV MAY	II MAY
21	Chlidonias niger	52.5	G	DEC - FEB	I OCT	II SEP	II MAY	IV APR
22	Ciconia nigra	49.7	F	NOV - JAN	II NOV	II OCT	IV APR	II APR
23	Circaetus gallicus	44.4	D	DEC - JAN	II OCT	IV SEP	II APR	IV MAR
24	Circus pygargus	46.7	E	NOV - JAN	II OCT	III SEP	I MAY	II APR
25	Clamator glandarius	40.2	B	NOV - DEC	IV SEP	III AGO	I APR	II MAR
26	Coracias garrulus	47.2	E	NOV - FEB	IV OCT	IV SEP	IV MAY	I MAY
27	Crex crex	54.1	H	NOV - FEB	IV NOV	III OCT	II MAY	III APR
28	Cuculus canorus	52.6	G	NOV - FEB	IV OCT	III SEP	I MAY	III APR
29	Delichon urbica	50	F	DEC - 15 JAN	II NOV	II OCT	III MAY	II APR
30	Emberiza hortulana	53.8	H	DEC - FEB	II OCT	IV SEP	III MAY	I MAY
...	continue							

	Species	Mean breeding lat. (decimal degrees)	Breeding lat. Group (see Figure 2)	Wintering window	Autumn migr. end	Mean aut. migr. (+- 2wks)	Spring migr. end	Mean spring migr. (+- 2wks)
	Continue from previous page							
31	Falco naumanni	44.6	D	NOV - JAN	IV OCT	IV SEP	II APR	III MAR
32	Falco subbuteo	48.6	E	NOV - FEB	II NOV	III OCT	IV MAY	I MAY
33	Falco vespertinus	54.3	H	NOV - FEB	I NOV	I OCT	II MAY	III APR
34	Ficedula hypoleuca	54.5	H	DEC - FEB	I OCT	IV AGO	I MAY	I APR
35	Glareola pratincola	38.5	B	NOV - JAN	III OCT	IV SEP	IV APR	II APR
36	Hieraaetus pennatus	43.2	C	NOV - JAN	III OCT	I OCT	IV APR	I APR
37	Hippolais polyglotta	42.7	C	DEC - FEB	IV OCT	III SEP	IV MAY	IV APR
38	Hirundo daurica	37.5	A	DEC - JAN	III OCT	IV SEP	IV APR	IV MAR
39	Hirundo rustica	52.5	G	DEC - JAN	IV NOV	II OCT	II MAY	I APR
40	Ixobrychus minutus	44.8	D	NOV - FEB	II NOV	I OCT	I MAY	III APR
41	Lanius collurio	51.5	G	NOV - FEB	II SEP	I SEP	I JUN	II MAY
42	Lanius minor	48.3	E	NOV - FEB	IV SEP	IV AGO	II MAY	I MAY
43	Lanius senator	41.8	C	NOV - FEB	II SEP	I SEP	III MAY	I MAY
44	Locustella luscinioides	47.7	E	NOV - FEB	III OCT	IV SEP	I MAY	I APR
45	Locustella naevia	54	H	NOV - FEB	III OCT	II SEP	II MAY	II APR
46	Luscinia megarhynchos	44.7	D	NOV - FEB	I SEP	III AGO	I MAY	III APR
47	Merops apiaster	46.3	E	NOV - FEB	III OCT	IV SEP	II MAY	III APR
48	Milvus migrans	47.1	E	NOV - 15 JAN	II OCT	II SEP	IV APR	IV MAR
49	Monticola saxatilis	42.8	C	DEC - FEB	I SEP	III AGO	IV APR*	I MAY
50	Motacilla flava	53.2	G	DEC - 15 FEB	I NOV	III SEP	II MAY	II APR
51	Muscicapa striata	52.7	G	DEC - FEB	I NOV	IV SEP	I JUN	I MAY
52	Neophron percnopterus	37.7	A	NOV - JAN	III SEP	I SEP	II MAY	II APR
53	Numenius phaeopus	63.1	K	DEC - JAN	II OCT	II SEP	II MAY	III APR
54	Nycticorax nycticorax	41.1	B	DEC - JAN	II NOV	II OCT	II APR	IV MAR
55	Oenanthe hispanica	37	A	NOV - FEB	III OCT	III SEP	I MAY	I APR
56	Oenanthe oenanthe	53.5	G	DEC - JAN	III OCT	IV SEP	I MAY	I APR
57	Oriolus oriolus	49.8	F	NOV - FEB	II SEP	IV AGO	II MAY	IV APR
58	Otus scops	46.7	E	DEC - JAN	I OCT	II SEP	IV APR	II APR
59	Pandion haliaetus	57.2	I	DEC - FEB	IV OCT	I OCT	IV APR	II APR
60	Pernis apivorus	52.8	G	NOV - FEB	IV OCT	IV SEP	I JUN	II MAY
61	Phoenicurus phoenicurus	53.2	G	DEC - JAN	IV OCT	IV SEP	I MAY	III APR
62	Phylloscopus bonelli	42	C	NOV - FEB	II SEP	III AGO	II MAY	I APR
63	Phylloscopus sibilatrix	54.1	H	NOV - FEB	II NOV	IV SEP	II MAY	IV APR
...	continue							

	Species	Mean breeding lat. (decimal degrees)	Breeding lat. Group (see Figure 2)	Wintering window	Autumn migr. end	Mean aut. migr. (+- 2wks)	Spring migr. end	Mean spring migr. (+- 2wks)
	Continue from previous page							
64	Phylloscopus trochilus	58	I	DEC - FEB	I NOV	III SEP	II MAY	III APR
65	Riparia riparia	53.2	G	DEC - 15 FEB	IV OCT	III SEP	I MAY	II APR
66	Saxicola rubetra	55.6	H	DEC - JAN	I NOV	I OCT	I MAY	II APR
67	Sterna albifrons	46.7	E	DEC - FEB	I OCT	II SEP	II MAY	IV APR
68	Sterna hirundo	53	G	DEC - FEB	I OCT	II SEP	I MAY	III APR
69	Sterna nilotica	45.7	D	DEC - JAN	I OCT	IV AGO	I MAY	III APR
70	Sterna paradisaea	65.2	L	NOV - FEB	III OCT	III SEP	II MAY	II APR
71	Streptopelia turtur	45.5	D	DEC - FEB	I NOV	I OCT	IV APR	I APR
72	Sylvia borin	55.2	H	DEC - FEB	II NOV	IV SEP	I JUN	IV APR
73	Sylvia cantillans	40.2	B	NOV - JAN	IV OCT	I OCT	IV APR	I APR
74	Sylvia communis	52.1	G	DEC - FEB	III OCT	II SEP	IV MAY	I MAY
75	Sylvia hortensis	40.2	B	DEC - FEB	IV SEP	IV AGO	II MAY	I APR
76	Tringa glareola	61.1	J	DEC - JAN	I OCT	II AGO	I MAY	III APR
77	Tringa nebularia	60	J	DEC - JAN	IV SEP	III AGO	IV APR	III APR

NOTES:
Winter windows are derived from Bernis (1980), Tellería (1981) and Finlaynson (1992)
Breeding latitudes and phenology of migration are derived from Cramp (1977-94), with the exception of : * SEO-Birdlife (2013); ** ICO (2013)

Cited Bibliography:

Bernis F (1980) La migración de las aves en el estrecho de Gibraltar. Vol. 1: Aves Planeadoras. Madrid: Universidad Complutense de Madrid.
Cramp S (ed) (1977- 1994) Handbook of the birds of Europe, the Middle East and North Africa – The birds of Western Palearctic. Oxford: Oxford University Press.
Finlayson JC (1992) Birds of the Strait of Gibraltar. London: T & AD Poyser.
ICO (2013) SIOC – Servidor d'informació ornitológica de Catalunya. http://www.sioc.cat/ Institut Catalá d'Ornitologia y Generalitat de Catalunya. Accessed: 10-01-2013
SEO-Birdlife (2013) Enciclopedia virtual de las aves de España www.enciclopediadelasaves.org . Sociedad Española de Ornitología, Madrid. Accessed: 10-01-2013
Tellería JL (1981) La migración de las Aves en el Estrecho de Gibraltar. Vol. 2, Aves No Planeadoras. Madrid: Universidad Complutense de Madrid.

Table S2, Chapter III

Results of the species-specific models, with parameters estimates and siginificance.

A: *"Model 1" series. In this series of models, temperatures for spring and autumn are calculated over the exact week of the end of migration while in Model 2 are calculated over the central week of migration ± a buffer of 2 weeks.(see Methods and Table S2). * indicates that the better model for the species was the one controlling for autoregression of lag 1. Significant results are marked in bold.*

	SPECIES	H1 ± S.E.	p	H1b ± S.E.	p	H2 ± S.E.	p	H3 ± S.E.	p	YEAR ± S.E.	p	AIC	General p of the model
1	Acrocephalus arundinaceus	0.038±0.054	0.483	0.059±0.055	0.289	-0.043±0.023	0.073	0.003±0.019	0.863	**0.015±0.004**	**0.002**	47.93	**0.014**
2	Acrocephalus paludicola	0.029±0.023	0.228	0.008±0.023	0.718	0.015±0.011	0.173	0.005±0.008	0.557	0.000±0.002	0.783	-4.185	0.312
3	Acrocephalus schoenobaenus	-0.052±0.058	0.371	0.026±0.060	0.664	-0.032±0.025	0.22	-0.020±0.030	0.51	**0.013±0.004**	**0.003**	43.505	**0.038**
4	Acrocephalus scirpaceus	-0.017±0.077	0.825	**0.200±0.077**	**0.015**	-0.064±0.033	0.058	-0.018±0.032	0.577	**0.031±0.006**	**0**	69.911	**<0.001**
5	Anas querquedula	-0.167±0.092	0.08	-0.055±0.091	0.546	-0.050±0.043	0.257	0.052±0.033	0.129	**0.047±0.009**	**0**	78.078	**<0.001**
6	Anthus campestris	0.106±0.082	0.202	**0.188±0.082**	**0.029**	0.015±0.033	0.659	-0.028±0.029	0.336	0.012±0.006	0.056	67.379	**0.046**
7	Anthus cervinus	-0.271±0.089	0.005	-0.120±0.089	0.185	-0.003±0.047	0.943	-0.010±0.028	0.713	0.010±0.018	0.594	80.546	**0.004***
8	Anthus trivialis	0.037±0.052	0.484	0.034±0.053	0.526	0.031±0.025	0.22	0.055±0.030	0.072	**0.010±0.004**	**0.017**	44.301	**0.02**
9	Apus apus	0.143±0.102	0.171	-0.008±0.101	0.935	-0.011±0.045	0.816	0.011±0.033	0.729	**0.036±0.008**	**0**	85.185	**<0.001**
10	Apus melba	0.063±0.075	0.408	**0.164±0.075**	**0.036**	0.029±0.034	0.389	0.036±0.032	0.276	0.005±0.006	0.417	65.597	**0.045**
11	Apus pallidus	0.101±0.100	0.316	0.207±0.103	0.053	0.002±0.043	0.963	-0.019±0.049	0.701	**0.022±0.008**	**0.009**	84.066	**0.014**
12	Ardea purpurea	0.015±0.077	0.848	0.151±0.077	0.059	-0.023±0.034	0.501	0.067±0.039	0.096	**0.046±0.007**	**0**	69.206	**<0.001**
13	Ardeola ralloides	-0.086±0.159	0.591	-0.058±0.166	0.729	-0.061±0.056	0.284	-0.015±0.063	0.811	**0.109±0.024**	**0**	110.463	**<0.001***
14	Calandrella brachydactyla	0.210±0.073	0.007	0.043±0.072	0.555	**-0.095±0.030**	**0.004**	0.002±0.032	0.939	0.017±0.008	0.061	65.305	**0.001***
15	Caprimulgus europaeus	-0.003±0.039	0.93	-0.023±0.038	0.546	-0.038±0.021	0.079	0.001±0.014	0.933	0.005±0.003	0.118	24.311	0.15
16	Caprimulgus ruficollis	-0.002±0.084	0.977	0.035±0.083	0.677	-0.047±0.044	0.294	0.023±0.037	0.536	0.001±0.006	0.826	70.413	0.866
17	Cercotrichas galactotes	0.102±0.039	0.013	0.023±0.040	0.575	-0.006±0.016	0.691	-0.006±0.014	0.654	0.004±0.003	0.163	23.013	0.07
18	Charadrius dubius	0.180±0.167	0.289	0.068±0.178	0.704	-0.007±0.06	0.908	-0.015±0.056	0.792	**0.107±0.024**	**0**	114.825	**<0.001***
19	Chlidonias hybrida	-0.086±0.109	0.439	-0.051±0.110	0.644	0.062±0.037	0.106	0.060±0.045	0.191	0.031±0.040	0.438	95.583	**<0.001***
20	Chlidonias leucopterus	-0.070±0.056	0.223	**-0.144±0.057**	**0.017**	0.009±0.020	0.649	-0.026±0.018	0.17	0.006±0.015	0.698	54.885	**0.002***
21	Chlidonias niger	0.055±0.086	0.524	0.149±0.088	0.098	0.002±0.034	0.96	-0.005±0.027	0.844	0.022±0.011	0.053	78.626	**0.006***
22	Ciconia nigra	-0.079±0.122	0.519	0.168±0.111	0.139	0.049±0.046	0.294	-0.048±0.037	0.2	**0.077±0.022**	**0.002**	89.813	**<0.001***
23	Circaetus gallicus	0.019±0.083	0.819	**-0.239±0.078**	**0.005**	**-0.091±0.035**	**0.015**	0.006±0.033	0.856	**0.051±0.006**	**0**	69.453	**<0.001**
24	Circus pygargus	0.079±0.081	0.339	0.034±0.081	0.68	0.010±0.035	0.77	-0.057±0.029	0.057	**0.029±0.009**	**0.003**	69.087	**0.001***
25	Clamator glandarius	-0.045±0.106	0.67	0.151±0.105	0.16	-0.014±0.053	0.799	-0.027±0.056	0.637	0.014±0.009	0.126	93.392	0.308
26	Coracias garrulus	**-0.050±0.023**	**0.036**	0.015±0.023	0.534	-0.007±0.009	0.426	-0.017±0.010	0.091	**0.005±0.002**	**0.006**	-11.699	**0.017**
27	Crex crex	0.011±0.040	0.78	-0.058±0.035	0.114	0.016±0.014	0.277	-0.013±0.016	0.42	0.004±0.002	0.139	14.605	0.112
28	Cuculus canorus	-0.013±0.048	0.785	**0.105±0.049**	**0.04**	-0.004±0.019	0.819	**-0.055±0.018**	**0.004**	**0.009±0.004**	**0.017**	35.163	**0.008**
29	Delichon urbica	0.045±0.092	0.626	0.126±0.089	0.169	-0.011±0.039	0.78	-0.065±0.038	0.096	**0.054±0.016**	**0.002**	86.792	**<0.001***
..	Continue ...												

	SPECIES	H1 ± S.E.	p	H1b ± S.E.	p	H2 ± S.E.	p	H3 ± S.E.	p	YEAR ± S.E.	p	AIC	General p of the model
	...continue from previous page...												
30	Emberiza hortulana	0.024±0.034	0.482	0.020±0.034	0.558	0.002±0.015	0.902	0.020±0.023	0.372	0.004±0.003	0.106	17.731	0.437
31	Falco naumanni	-0.210±0.211	0.326	0.065±0.207	0.756	-0.003±0.081	0.972	0.124±0.083	0.147	**0.041±0.015**	**0.01**	125.233	0.061
32	Falco subbuteo	0.070±0.082	0.399	0.111±0.075	0.147	0.004±0.033	0.905	0.044±0.033	0.184	**0.025±0.006**	**0**	60.952	**<0.001**
33	Falco vespertinus	-0.002±0.065	0.981	-0.012±0.062	0.852	-0.012±0.032	0.714	0.011±0.027	0.682	**0.014±0.004**	**0.003**	48.752	**0.038**
34	Ficedula hypoleuca	0.010±0.063	0.87	-0.011±0.062	0.861	0.001±0.027	0.962	-0.017±0.032	0.6	**0.018±0.005**	**0.001**	55.754	**0.021**
35	Glareola pratincola	-0.053±0.058	0.37	0.079±0.058	0.181	0.013±0.025	0.604	0.009±0.023	0.693	0.002±0.005	0.636	46.593	0.473
36	Hieraaetus pennatus	0.108±0.142	0.451	0.014±0.144	0.923	0.029±0.063	0.649	-0.025±0.050	0.617	**0.180±0.024**	**0**	105.41	**<0.001***
37	Hippolais polyglotta	-0.008±0.038	0.839	-0.033±0.038	0.384	-0.014±0.015	0.356	0.014±0.017	0.43	0.002±0.005	0.723	24.437	0.262*
38	Hirundo daurica	-0.097±0.087	0.274	0.143±0.087	0.112	0.021±0.039	0.591	-0.05±0.033	0.142	**0.043±0.007**	**0**	75.489	**<0.001**
39	Hirundo rustica	0.092±0.178	0.61	0.199±0.172	0.254	0.009±0.059	0.881	0.083±0.051	0.115	**0.099±0.021**	**0**	119.919	**<0.001***
40	Ixobrychus minutus	-0.101±0.105	0.346	-0.163±0.105	0.132	-0.048±0.037	0.199	-0.049±0.033	0.154	**0.094±0.045**	**0.045**	87.519	**<0.001***
41	Lanius collurio	-0.014±0.025	0.581	-0.025±0.027	0.371	-0.011±0.010	0.301	0.009±0.008	0.241	0.003±0.002	0.118	-4.782	0.277
42	Lanius minor	0.103±0.046	0.031	0.045±0.046	0.337	0.012±0.020	0.549	-0.005±0.016	0.755	0.003±0.003	0.397	30.848	0.151
43	Lanius senator	-0.004±0.070	0.956	0.097±0.071	0.184	-0.011±0.028	0.686	0.034±0.031	0.283	**0.017±0.005**	**0.002**	58.039	**0.004**
44	Locustella luscinioides	0.054±0.032	0.097	0.009±0.032	0.778	**-0.032±0.014**	**0.025**	-0.007±0.011	0.532	0.003±0.002	0.212	7.102	0.147
45	Locustella naevia	0.002±0.071	0.98	-0.083±0.070	0.247	-0.013±0.030	0.665	0.015±0.031	0.638	-0.006±0.005	0.225	56.523	0.512
46	Luscinia megarhynchos	-0.019±0.064	0.769	0.073±0.063	0.257	-0.006±0.034	0.861	-0.008±0.023	0.721	0.008±0.004	0.069	50.728	0.382
47	Merops apiaster	0.083±0.048	0.094	0.076±0.048	0.125	-0.005±0.020	0.809	0.001±0.017	0.951	0.006±0.004	0.077	32.605	0.085
48	Milvus migrans	-0.037±0.080	0.644	-0.070±0.077	0.366	-0.067±0.036	0.071	0.028±0.035	0.422	**0.078±0.007**	**0**	68.29	**0**
49	Monticola saxatilis	-0.004±0.048	0.928	-0.021±0.047	0.662	-0.004±0.027	0.871	0.013±0.023	0.584	0.001±0.004	0.861	38.496	0.971
50	Motacilla flava	**0.235±0.113**	**0.045**	**0.242±0.112**	**0.039**	0.035±0.061	0.577	-0.008±0.034	0.811	**0.054±0.017**	**0.003**	96.523	**<0.001***
51	Muscicapa striata	-0.059±0.051	0.257	0.012±0.052	0.812	-0.029±0.028	0.301	0.002±0.017	0.885	-0.002±0.004	0.651	42.739	0.574
52	Neophron percnopterus	-0.107±0.102	0.299	-0.159±0.103	0.132	-0.037±0.037	0.32	0.026±0.037	0.484	**0.049±0.007**	**0**	82.992	**<0.001**
53	Numenius phaeopus	0.098±0.113	0.393	**0.297±0.113**	**0.013**	0.022±0.042	0.596	-0.042±0.037	0.257	0.075±0.040	0.066	97.215	**<0.001***
54	Nycticorax nycticorax	-0.046±0.108	0.669	0.122±0.105	0.255	-0.040±0.040	0.32	-0.052±0.045	0.257	**0.072±0.017**	**0**	87.793	**<0.001***
55	Oenanthe hispanica	-0.086±0.065	0.197	**0.134±0.062**	**0.039**	-0.013±0.027	0.626	0.028±0.026	0.278	0.002±0.004	0.734	48.877	0.189
56	Oenanthe oenanthe	**-0.141±0.068**	**0.048**	-0.038±0.067	0.575	-0.016±0.031	0.613	0.034±0.026	0.196	**0.022±0.006**	**0.001**	60.139	**<0.001**
57	Oriolus oriolus	-0.062±0.051	0.225	**-0.114±0.051**	**0.034**	-0.013±0.020	0.53	**-0.043±0.016**	**0.01**	**0.011±0.004**	**0.005**	38.417	**0.002**
58	Otus scops	0.072±0.079	0.371	-0.098±0.079	0.227	0.047±0.036	0.205	-0.072±0.038	0.067	**0.036±0.008**	**0**	69.785	**<0.001**
59	Pandion haliaetus	-0.098±0.133	0.467	0.251±0.136	0.074	-0.007±0.049	0.891	-0.021±0.057	0.713	**0.131±0.037**	**0.001**	106.218	**<0.001***
60	Pernis apivorus	-0.015±0.061	0.812	-0.099±0.069	0.162	0.050±0.025	0.061	0.001±0.020	0.955	**0.025±0.005**	**0**	50.496	**<0.001**
61	Phoenicurus phoenicurus	0.076±0.070	0.285	0.079±0.070	0.27	0.017±0.030	0.567	-0.013±0.027	0.63	0.005±0.006	0.424	62.611	0.477
62	Phylloscopus bonelli	0.078±0.046	0.098	0.071±0.046	0.128	-0.010±0.018	0.572	0.007±0.021	0.73	0.004±0.003	0.277	30.895	0.188
63	Phylloscopus sibilatrix	-0.024±0.016	0.134	**0.032±0.015**	**0.034**	0.008±0.006	0.213	0.005±0.006	0.446	0.000±0.001	0.794	-40.805	0.084
64	Phylloscopus trochilus	0.048±0.041	0.246	0.008±0.039	0.846	0.022±0.022	0.313	-0.022±0.020	0.292	0.003±0.003	0.403	27.392	0.26
65	Riparia riparia	0.090±0.123	0.469	-0.001±0.122	0.997	-0.059±0.054	0.283	0.057±0.050	0.262	**0.053±0.011**	**0**	100.476	**<0.001**
66	Saxicola rubetra	**-0.157±0.070**	**0.032**	0.099±0.068	0.158	0.008±0.038	0.833	-0.039±0.034	0.267	**0.020±0.005**	**0.001**	59.702	**0.002**
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	SPECIES	H1 ± S.E.	p	H1b ± S.E.	p	H2 ± S.E.	p	H3 ± S.E.	p	YEAR ± S.E.	p	AIC	General p of the model
	...continue from previous page...												
67	Sterna albifrons	0.053±0.091	0.562	-0.077±0.093	0.409	-0.066±0.040	0.112	0.042±0.036	0.254	0.009±0.007	0.231	80.257	0.171
68	Sterna hirundo	0.117±0.092	0.212	0.151±0.092	0.109	-0.027±0.040	0.513	0.019±0.036	0.612	**0.024±0.008**	**0.004**	80.257	**0.004**
69	Sterna nilotica	-0.138±0.071	0.062	0.014±0.070	0.846	**-0.074±0.030**	**0.02**	0.014±0.027	0.609	**0.020±0.005**	**0.001**	62.567	**0.001**
70	Sterna paradisaea	**0.140±0.068**	**0.048**	0.025±0.067	0.719	-0.011±0.029	0.715	0.021±0.026	0.428	**0.011±0.005**	**0.031**	53.951	0.073
71	Streptopelia turtur	0.007±0.064	0.913	0.014±0.065	0.828	-0.022±0.034	0.528	-0.024±0.027	0.379	0.016±0.008	0.067	57.427	**0.016***
72	Sylvia borin	-0.022±0.035	0.547	0.009±0.038	0.813	0.024±0.015	0.122	0.023±0.017	0.179	0.002±0.003	0.534	20.523	0.318
73	Sylvia cantillans	0.029±0.047	0.541	-0.016±0.048	0.739	-0.003±0.020	0.896	0.006±0.020	0.772	**0.010±0.004**	**0.01**	35.241	0.051
74	Sylvia communis	0.021±0.032	0.524	-0.003±0.032	0.936	0.023±0.015	0.138	-0.008±0.012	0.517	0.001±0.003	0.566	14.568	0.378
75	Sylvia hortensis	-0.026±0.037	0.485	-0.006±0.037	0.876	-0.006±0.017	0.739	-0.021±0.016	0.21	0.000±0.003	0.933	23.37	0.753
76	Tringa glareola	-0.087±0.126	0.495	0.184±0.122	0.142	-0.041±0.054	0.45	-0.013±0.055	0.811	**0.082±0.009**	**0**	96.761	**<0.001**
77	Tringa nebularia	0.063±0.224	0.781	0.197±0.216	0.369	0.014±0.095	0.882	0.007±0.090	0.942	**0.102±0.027**	**0.001**	132.924	**<0.001***

B: *"Model 2" series. In this series of models, temperatures for spring and autumn are calculated over the calculated over the central week of migration ± a buffer of 2 weeks (see Methods and Table S2). * indicates that the better model for the species was the one controlling for autoregression of lag 1. Significant results are marked in bold.*

	SPECIES	H1 ± S.E.	p	H1b ± S.E.	p	H2 ± S.E.	p	H3 ± S.E.	p	YEAR ± S.E.	p	AIC	General p of the model
1	Acrocephalus arundinaceus	0.034±0.048	0.483	0.063±0.048	0.2	**-0.067±0.031**	**0.038**	0.082±0.044	0.072	0.006±0.006	0.266	37.341	**<0.001**
2	Acrocephalus paludicola	0.035±0.024	0.161	0.008±0.026	0.756	0.004±0.017	0.819	-0.005±0.026	0.835	0.001±0.002	0.609	-5.006	0.68
3	Acrocephalus schoenobaenus	-0.086±0.061	0.169	0.006±0.057	0.92	0.003±0.036	0.927	-0.053±0.074	0.474	**0.014±0.005**	**0.015**	42.197	0.063
4	Acrocephalus scirpaceus	0.004±0.078	0.96	**0.191±0.078**	**0.021**	-0.035±0.051	0.503	0.052±0.056	0.362	**0.022±0.008**	**0.013**	69.285	**<0.001**
5	Anas querquedula	**-0.205±0.091**	**0.032**	-0.066±0.099	0.512	-0.063±0.059	0.289	0.063±0.074	0.397	**0.049±0.010**	**0**	77.645	**<0.001**
6	Anthus campestris	0.103±0.081	0.213	**0.178±0.084**	**0.042**	-0.038±0.048	0.441	-0.004±0.051	0.942	0.010±0.008	0.194	65.935	0.059
7	Anthus cervinus	**-0.201±0.095**	**0.043**	0.006±0.095	0.953	**-0.234±0.061**	**0.001**	-0.098±0.075	0.203	**0.016±0.007**	**0.025**	65.318	**<0.001***
8	Anthus trivialis	0.035±0.058	0.549	0.061±0.055	0.277	0.021±0.037	0.581	0.007±0.076	0.929	0.010±0.006	0.084	46.025	0.135
9	Apus apus	0.154±0.097	0.123	0.024±0.099	0.814	-0.008±0.065	0.906	0.148±0.094	0.126	**0.025±0.010**	**0.022**	79.783	**<0.001**
10	Apus melba	0.091±0.071	0.209	0.136±0.070	0.062	-0.084±0.046	0.077	-0.031±0.056	0.586	0.010±0.007	0.144	61.015	**0.014**
11	Apus pallidus	0.101±0.115	0.384	**0.206±0.101**	**0.05**	-0.037±0.068	0.59	0.008±0.060	0.896	**0.021±0.009**	**0.024**	82.406	**0.011**
12	Ardea purpurea	-0.007±0.080	0.932	**0.170±0.080**	**0.04**	0.052±0.052	0.322	0.081±0.089	0.369	**0.047±0.008**	**0**	67.771	**<0.001**
13	Ardeola ralloides	-0.076±0.189	0.691	0.043±0.184	0.816	-0.119±0.111	0.289	-0.208±0.173	0.24	**0.120±0.014**	**0**	107.591	**<0.001***
14	Calandrella brachydactyla	**0.292±0.092**	**0.003**	0.074±0.078	0.354	-0.007±0.051	0.895	**-0.113±0.051**	**0.035**	0.016±0.009	0.106	67.146	**0.003**
15	Caprimulgus europaeus	-0.012±0.037	0.756	-0.037±0.039	0.352	**-0.055±0.024**	**0.028**	-0.017±0.037	0.652	0.006±0.003	0.059	20.808	0.093
16	Caprimulgus ruficollis	-0.002±0.075	0.976	-0.003±0.075	0.964	**-0.112±0.050**	**0.031**	0.027±0.066	0.687	0.002±0.007	0.761	64.414	0.221
17	Cercotrichas galactotes	**0.099±0.040**	**0.019**	0.027±0.040	0.506	-0.005±0.024	0.839	0.005±0.025	0.844	0.003±0.003	0.35	21.063	0.08
18	Charadrius dubius	0.103±0.192	0.597	0.158±0.206	0.447	-0.024±0.118	0.843	0.035±0.153	0.821	**0.109±0.014**	**0**	112.11	**<0.001***
19	Chlidonias hybrida	-0.013±0.178	0.943	0.130±0.178	0.471	0.003±0.120	0.978	-0.146±0.175	0.41	**0.056±0.016**	**0.001**	93.856	**<0.001***
20	Chlidonias leucopterus	-0.015±0.076	0.847	-0.054±0.076	0.482	-0.006±0.053	0.908	-0.014±0.060	0.813	0.013±0.007	0.083	49.374	**<0.001***
21	Chlidonias niger	0.055±0.095	0.563	0.164±0.094	0.091	0.012±0.065	0.85	0.023±0.072	0.747	**0.020±0.009**	**0.038**	75.59	**0.005**
22	Ciconia nigra	-0.087±0.135	0.522	0.049±0.143	0.732	0.010±0.082	0.903	-0.106±0.139	0.451	**0.087±0.012**	**0**	87.941	**<0.001***
23	Circaetus gallicus	0.026±0.083	0.756	**-0.252±0.077**	**0.003**	**-0.129±0.050**	**0.015**	-0.037±0.053	0.498	**0.050±0.007**	**0**	66.52	**<0.001**
24	Circus pygargus	0.115±0.079	0.153	-0.023±0.085	0.786	0.003±0.049	0.949	**-0.193±0.081**	**0.024**	**0.034±0.009**	**0.001**	65.886	**0.001**
25	Clamator glandarius	-0.019±0.126	0.881	0.164±0.105	0.128	-0.019±0.104	0.854	0.019±0.087	0.826	0.012±0.013	0.375	90.733	0.265
26	Coracias garrulus	**-0.059±0.022**	**0.01**	0.012±0.022	0.592	0.003±0.013	0.827	0.012±0.014	0.411	**0.003±0.001**	**0.033**	-10.879	0.056
27	Crex crex	0.032±0.038	0.412	-0.067±0.036	0.072	0.015±0.023	0.528	0.007±0.048	0.892	0.003±0.004	0.419	12.684	0.18
28	Cuculus canorus	-0.031±0.052	0.552	0.084±0.052	0.114	-0.020±0.030	0.518	**-0.118±0.047**	**0.017**	**0.013±0.005**	**0.009**	36.299	0.053
29	Delichon urbica	0.023±0.109	0.837	0.106±0.120	0.382	-0.018±0.079	0.82	0.001±0.142	0.994	**0.061±0.013**	**0**	86.53	**<0.001***
30	Emberiza hortulana	0.025±0.034	0.463	0.027±0.034	0.423	-0.001±0.022	0.974	0.017±0.033	0.617	0.004±0.003	0.182	17.009	0.571
31	Falco naumanni	-0.324±0.205	0.123	0.182±0.192	0.35	0.018±0.116	0.875	**0.299±0.124**	**0.022**	0.026±0.017	0.142	118.678	**0.006**
32	Falco subbuteo	**0.141±0.064**	**0.036**	0.126±0.063	0.056	**-0.130±0.039**	**0.002**	**0.090±0.041**	**0.035**	**0.026±0.005**	**0**	49.459	**<0.001**
33	Falco vespertinus	-0.019±0.065	0.776	-0.011±0.062	0.863	-0.011±0.039	0.773	-0.019±0.08	0.813	**0.015±0.006**	**0.015**	46.524	**0.042**
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	SPECIES	H1 ± S.E.	p	H1b ± S.E.	p	H2 ± S.E.	p	H3 ± S.E.	p	YEAR ± S.E.	p	AIC	General p of the model
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34	Ficedula hypoleuca	0.054±0.058	0.363	0.006±0.057	0.911	-0.058±0.044	0.197	0.062±0.058	0.292	**0.017±0.004**	**0**	51.197	**0.009**
35	Glareola pratincola	-0.051±0.057	0.378	0.087±0.056	0.132	0.032±0.035	0.366	-0.043±0.049	0.381	0.005±0.004	0.239	43.336	0.327
36	Hieraaetus pennatus	-0.041±0.175	0.819	-0.073±0.170	0.671	-0.044±0.107	0.684	0.035±0.179	0.847	**0.185±0.014**	**0**	103.034	**<0.001***
37	Hippolais polyglotta	0.014±0.036	0.708	-0.010±0.036	0.791	**-0.049±0.024**	**0.046**	-0.056±0.037	0.146	0.004±0.003	0.207	15.082	**0.014**
38	Hirundo daurica	-0.095±0.091	0.303	0.128±0.089	0.16	0.020±0.058	0.733	0.055±0.081	0.506	**0.037±0.009**	**0**	74.791	**<0.001**
39	Hirundo rustica	0.131±0.189	0.494	0.298±0.203	0.152	-0.013±0.118	0.911	0.165±0.157	0.302	**0.100±0.015**	**0**	117.772	**<0.001***
40	Ixobrychus minutus	-0.123±0.169	0.473	-0.034±0.170	0.845	**-0.339±0.103**	**0.003**	0.038±0.102	0.711	**0.124±0.012**	**0**	88.117	**<0.001***
41	Lanius collurio	-0.015±0.024	0.53	-0.009±0.024	0.699	-0.026±0.015	0.098	-0.023±0.017	0.173	**0.005±0.002**	**0.013**	-8.349	0.184
42	Lanius minor	**0.111±0.044**	**0.017**	0.054±0.045	0.238	-0.018±0.033	0.59	0.030±0.030	0.312	0.001±0.004	0.77	27.563	0.099
43	Lanius senator	0.021±0.067	0.751	0.070±0.071	0.33	0.013±0.042	0.76	0.079±0.055	0.165	0.014±0.007	0.06	55.29	**0.003**
44	Locustella luscinioides	0.046±0.031	0.145	-0.001±0.032	0.968	-0.020±0.019	0.289	0.013±0.019	0.515	0.000±0.003	0.992	6.077	0.206
45	Locustella naevia	0.033±0.065	0.613	-0.075±0.065	0.259	-0.057±0.040	0.161	0.129±0.078	0.109	-0.012±0.007	0.07	49.902	0.114
46	Luscinia megarhynchos	0.050±0.054	0.364	0.051±0.056	0.371	**0.168±0.043**	**0.001**	0.046±0.035	0.196	0.000±0.007	0.957	40.355	**0.015**
47	Merops apiaster	0.078±0.045	0.097	0.069±0.047	0.151	-0.006±0.028	0.817	-0.039±0.041	0.341	**0.008±0.004**	**0.03**	29.17	0.055
48	Milvus migrans	-0.057±0.079	0.472	-0.086±0.083	0.307	-0.048±0.053	0.381	-0.006±0.052	0.902	**0.081±0.008**	**0**	69.669	**<0.001**
49	Monticola saxatilis	-0.001±0.045	0.983	-0.016±0.045	0.735	**0.085±0.039**	**0.039**	-0.011±0.040	0.779	-0.001±0.005	0.879	34.726	0.764
50	Motacilla flava	0.199±0.120	0.109	0.125±0.130	0.346	-0.137±0.080	0.099	-0.134±0.136	0.333	**0.061±0.012**	**0**	92.392	**<0.001***
51	Muscicapa striata	-0.070±0.050	0.166	0.015±0.050	0.767	-0.030±0.033	0.378	-0.002±0.032	0.95	-0.002±0.004	0.727	41.342	0.633
52	Neophron percnopterus	-0.108±0.098	0.279	-0.157±0.098	0.122	-0.030±0.061	0.629	-0.128±0.078	0.11	**0.057±0.007**	**0**	80.299	**<0.001**
53	Numenius phaeopus	0.083±0.189	0.663	0.315±0.178	0.086	**-0.255±0.117**	**0.037**	-0.140±0.159	0.385	**0.101±0.015**	**0**	95.765	**<0.001***
54	Nycticorax nycticorax	-0.034±0.122	0.78	0.123±0.116	0.296	**-0.154±0.073**	**0.044**	-0.004±0.114	0.974	**0.081±0.011**	**0**	84.166	**<0.001***
55	Oenanthe hispanica	-0.092±0.059	0.131	0.112±0.059	0.07	-0.002±0.035	0.959	0.101±0.051	0.057	-0.003±0.005	0.577	44.493	0.068
56	Oenanthe oenanthe	-0.128±0.065	0.058	0.002±0.068	0.979	-0.065±0.040	0.111	0.105±0.052	0.053	**0.021±0.004**	**0**	56.194	**<0.001**
57	Oriolus oriolus	-0.061±0.055	0.279	**-0.127±0.056**	**0.032**	-0.013±0.042	0.766	-0.041±0.039	0.303	**0.012±0.005**	**0.023**	41.245	**0.025**
58	Otus scops	0.104±0.090	0.259	-0.201±0.100	0.053	-0.047±0.060	0.439	-0.112±0.108	0.311	**0.031±0.009**	**0.001**	73.46	**0.003**
59	Pandion haliaetus	0.043±0.183	0.816	**0.410±0.180**	**0.03**	**-0.287±0.127**	**0.031**	-0.045±0.224	0.844	**0.145±0.017**	**0**	103.096	**<0.001***
60	Pernis apivorus	-0.014±0.060	0.823	-0.073±0.062	0.247	0.019±0.037	0.618	**-0.084±0.040**	**0.044**	**0.034±0.006**	**0**	47.561	**<0.001**
61	Phoenicurus phoenicurus	0.093±0.062	0.147	0.090±0.064	0.169	**-0.102±0.041**	**0.019**	0.061±0.061	0.322	0.000±0.007	0.968	52.378	**0.02**
62	Phylloscopus bonelli	0.049±0.045	0.281	0.079±0.044	0.082	-0.009±0.037	0.805	0.063±0.046	0.185	0.002±0.003	0.582	26.469	0.111
63	Phylloscopus sibilatrix	-0.011±0.013	0.413	**0.030±0.013**	**0.032**	0.012±0.008	0.133	**0.034±0.013**	**0.015**	-0.001±0.001	0.314	-47.941	**0.009**
64	Phylloscopus trochilus	0.039±0.042	0.35	0.000±0.039	0.995	0.009±0.026	0.74	-0.086±0.049	0.09	0.006±0.004	0.116	24.452	0.194
65	Riparia riparia	0.078±0.123	0.53	-0.035±0.132	0.796	-0.095±0.083	0.259	-0.052±0.137	0.71	**0.057±0.013**	**0**	97.576	**<0.001**
66	Saxicola rubetra	**-0.140±0.065**	**0.041**	0.076±0.067	0.267	-0.006±0.045	0.891	-0.121±0.089	0.18	**0.023±0.008**	**0.006**	55.71	**0.001**
67	Sterna albifrons	0.028±0.092	0.764	-0.078±0.092	0.402	-0.049±0.063	0.44	-0.067±0.069	0.341	0.015±0.010	0.139	79.911	0.363
68	Sterna hirundo	0.107±0.092	0.254	0.124±0.090	0.176	-0.033±0.062	0.593	0.034±0.086	0.694	0.022±0.011	0.051	77.136	**0.003**
69	Sterna nilotica	-0.138±0.076	0.081	0.026±0.072	0.717	0.110±0.055	0.055	0.012±0.050	0.82	0.017±0.009	0.06	63.226	**0.005**
70	Sterna paradisaea	0.130±0.068	0.063	0.019±0.067	0.774	-0.037±0.039	0.358	0.014±0.049	0.778	0.009±0.005	0.073	51.765	0.063
...	continue												

	SPECIES	H1 ± S.E.	p	H1b ± S.E.	p	H2 ± S.E.	p	H3 ± S.E.	p	YEAR ± S.E.	p	AIC	General p of the model
	Continue from previous page												
71	Streptopelia turtur	-0.053±0.065	0.419	0.000±0.061	0.999	0.020±0.039	0.617	0.093±0.049	0.069	0.012±0.008	0.124	53.513	**0.005**
72	Sylvia borin	-0.017±0.035	0.624	0.061±0.036	0.097	0.017±0.022	0.461	-0.003±0.036	0.928	0.003±0.005	0.541	19.035	0.499
73	Sylvia cantillans	0.029±0.045	0.525	-0.007±0.045	0.886	0.023±0.028	0.422	0.033±0.040	0.422	0.010±0.005	0.059	31.696	**0.033**
74	Sylvia communis	0.030±0.033	0.373	0.006±0.033	0.856	-0.002±0.023	0.94	-0.001±0.021	0.979	0.002±0.003	0.486	15.47	0.827
75	Sylvia hortensis	-0.010±0.037	0.788	0.000±0.037	0.991	0.041±0.029	0.162	-0.028±0.037	0.457	-0.001±0.004	0.812	21.008	0.818
76	Tringa glareola	-0.044±0.121	0.718	0.157±0.116	0.187	0.127±0.086	0.15	0.040±0.103	0.7	**0.073±0.014**	**0**	93.063	**<0.001**
77	Tringa nebularia	0.062±0.225	0.783	0.194±0.214	0.373	-0.132±0.185	0.48	0.053±0.189	0.783	**0.104±0.029**	**0.001**	129.335	**<0.001***

Table S1, Chapter IV

List of trans-Saharan species studied and their results for the centre of abundance and northern edge of their recently established wintering areas in the western Mediterranean. For both parameters the number (n), the first and the last years with winter occurrences of the species are shown. For the centre of abundance, results from linear regressions between latitude and longitude centres with year are shown as the regression coefficients (slopes), correlation coefficients (r), and p-values (p). Positive slopes mean northward or eastward, respectively, displacements. These pairs of slopes were used to calculate a vector and angle to estimate the direction and rate of displacement of the centre of abundance. Absolute displacement in latitude and longitude attained during the period with available data for each species are also shown, as well as its derivate vector. For the northern edge, results from linear regressions between latitude of the 75th percentile of data and year are shown as the regression coefficients (slopes), correlation coefficients (r), and p-values (p). Positive slopes mean northward displacement. The absolute displacement is also shown. Because of the dimensions , table is given in part both for records and for columns.

PART I/III

Species	**CENTRE OF ABUNDANCE**													
	n	First year	Last year	*LATITUDE*			*LONGITUDE*			Vector (Slope)	Angle (degrees)	Latitude displacement (km)	Longitude displacement (km)	Vector (displacement)
				Slope (km/yr)	r	p	Slope (km/yr)	r	p					
Acrocephalus arundinaceus	13	1977	2004	26.317	0.511	0.074	24.871	0.438	0.135	36.210	46.62	710.6	671.5	977.7
Acrocephalus schoenobaenus	12	1980	2005	18.229	0.386	0.215	11.458	0.291	0.360	21.531	57.85	455.7	286.5	538.3
Acrocephalus scirpaceus	23	1975	2006	18.763	0.447	0.032	8.162	0.203	0.353	20.461	66.49	581.6	253.0	634.3
Anas querquedula	21	1984	2006	22.803	0.589	0.005	7.667	0.180	0.423	24.058	71.42	501.7	222.4	548.7
Anthus campestris	13	1978	2004	30.669	0.499	0.082	7.479	0.290	0.360	31.568	76.30	797.4	194.5	820.8
Anthus cervinus	22	1969	2005	4.303	0.113	0.617	-9.356	-0.443	0.051	10.298	294.70	154.9	-308.7	345.4
Apus apus	24	1971	2006	23.717	0.550	0.005	4.074	0.086	0.689	24.065	80.25	830.1	142.6	842.3
Apus pallidus	14	1982	2006	47.055	0.589	0.027	18.785	0.753	0.005	50.666	68.24	1129.3	450.8	1216.0
Ardea purpurea	24	1971	2006	23.125	0.649	0.001	16.124	0.403	0.051	28.192	55.11	809.4	564.3	986.7
Ardeola ralloides	25	1972	2006	8.859	0.417	0.038	-2.141	-0.084	0.690	9.114	346.41	301.2	-72.8	309.9
Calandrella brachydactyla	15	1969	2006	13.156	0.373	0.171	2.600	0.142	0.613	13.410	78.82	486.8	96.2	496.2
Calidris ferruginea	19	1975	2006	16.118	0.268	0.268	0.506	0.012	0.960	16.126	88.20	499.7	15.7	499.9
Caprimulgus ruficollis	18	1972	2004	19.961	0.497	0.036	8.221	0.334	0.176	21.588	67.61	638.8	263.1	690.8
Charadrius dubius	29	1977	2006	-2.941	-0.096	0.620	6.536	0.265	0.191	7.167	114.22	-85.3	189.6	207.9
Chlidonias hybrida	23	1972	2006	12.759	0.492	0.017	6.393	0.224	0.305	14.271	63.39	433.8	217.4	485.2
Chlidonias leucopterus	10	1989	2004	29.969	0.767	0.451	13.644	0.512	0.130	32.929	65.52	449.5	204.7	493.9
Chlidonias niger	24	1974	2006	-1.939	-0.052	0.811	2.420	0.083	0.700	3.101	128.71	-62.1	77.4	99.2
Ciconia nigra	25	1970	2006	10.226	0.330	0.107	5.582	-0.208	0.330	11.651	61.37	368.1	161.9	402.2
Circaetus gallicus	20	1971	2006	6.154	0.425	0.062	-5.080	-0.137	0.554	7.980	320.46	215.4	-177.8	279.3
Circus pygargus	13	1986	2006	21.108	0.329	0.272	-27.044	-0.366	0.219	34.306	307.97	422.2	-540.9	686.1
...continue...														

Species	CENTRE OF ABUNDANCE													
	n	First year	Last year	LATITUDE			LONGITUDE			Vector (Slope)	Angle (degrees)	Latitude displacement (km)	Longitude displacement (km)	Vector (displacement)
				Slope (km/yr)	r	p	Slope (km/yr)	r	p					
Continue from previous page														
Clamator glandarius	16	1970	2006	3.663	0.111	0.683	1.377	-0.319	0.247	3.913	69.40	131.9	44.1	139.0
Cuculus canorus	10	1979	2006	17.175	0.608	0.062	2.845	0.073	0.841	17.409	80.59	463.7	76.8	470.0
Delichon urbica	25	1970	2006	14.449	0.647	0.000	-5.640	-0.260	0.220	15.510	338.68	520.1	-197.4	556.3
Falco naumanni	26	1972	2006	5.074	0.198	0.332	2.017	0.343	0.101	5.460	68.32	172.5	68.6	185.6
Falco subbuteo	23	1969	2006	20.521	0.566	0.005	0.400	0.012	0.957	20.525	88.88	759.3	14.8	759.4
Falco vespertinus	10	1982	2004	7.846	0.205	0.570	9.640	0.232	0.518	12.429	39.14	172.6	212.1	273.4
Ficedula hypoleuca	12	1977	2006	10.132	0.361	0.249	10.258	0.238	0.434	14.418	44.64	293.8	297.5	418.1
Hieraaetus pennatus	28	1969	2006	14.760	0.627	0.000	16.657	0.631	0.000	22.256	41.54	546.1	616.3	823.5
Hippolais polyglotta	10	1972	1999	16.238	0.294	0.409	29.895	0.623	0.054	34.021	28.51	438.4	807.2	918.6
Hirundo daurica	17	1983	2006	20.129	0.447	0.072	-6.341	-0.195	0.452	21.104	342.52	463.0	-145.8	485.4
Hirundo rustica	27	1971	2006	17.642	0.512	0.006	6.738	0.239	0.240	18.885	69.10	617.5	229.1	658.6
Ixobrychus minutus	20	1987	2006	15.536	0.777	0.000	46.826	0.885	0.000	49.336	18.36	295.2	1217.5	1252.8
Lanius senator	15	1988	2005	44.919	0.689	0.004	30.251	0.453	0.078	54.156	56.04	763.6	635.3	993.3
Locustella naevia	10	1971	2003	20.710	0.655	0.040	19.125	0.578	0.080	28.190	47.28	662.7	612.0	902.1
Milvus migrans	28	1969	2006	22.192	0.693	0.000	7.746	0.268	0.168	23.505	70.76	821.1	286.6	869.7
Motacilla flava	28	1969	2006	11.804	0.499	0.007	9.001	0.436	0.023	14.844	52.67	436.7	333.0	549.2
Muscicapa striata	16	1970	2006	17.624	0.561	0.024	19.847	0.600	0.014	26.542	41.60	634.5	714.5	955.5
Neophron percnopterus	20	1980	2006	14.261	0.453	0.045	-15.155	-0.343	0.139	20.809	313.26	370.8	-394.0	541.0
Numenius phaeopus	29	1972	2006	-4.080	-0.103	0.594	-26.554	-0.659	0.000	26.865	261.26	-138.7	-902.8	913.4
Nycticorax nycticorax	26	1975	2006	27.926	0.762	0.000	18.215	0.478	0.013	33.341	56.88	865.7	564.7	1033.6
Oenanthe oenanthe	15	1972	2004	24.016	0.390	0.151	19.315	0.362	0.185	30.820	51.19	768.5	618.1	986.2
Oriolus oriolus	11	1975	2006	9.543	0.479	0.136	-45.990	-0.944	0.000	46.969	281.72	295.8	-1287.7	1321.3
Otus scops	19	1972	2006	21.849	0.604	0.006	22.003	0.554	0.014	31.008	44.80	742.9	748.1	1054.3
Pandion haliaetus	28	1973	2006	15.003	0.444	0.018	18.030	0.572	0.001	23.456	39.76	495.1	595.0	774.0
Pernis apivorus	19	1977	2006	6.426	0.203	0.405	-13.582	-0.356	0.135	15.025	295.32	186.4	-393.9	435.7
Riparia riparia	17	1990	2006	35.135	0.515	0.035	-4.962	-0.093	0.724	35.484	351.96	562.2	-79.4	567.7
Saxicola rubetra	20	1969	2006	25.995	0.730	0.000	15.216	0.454	0.044	30.121	59.66	961.8	563.0	1114.5
Sterna albifrons	19	1972	2006	18.474	0.529	0.020	9.672	0.320	0.182	20.852	62.37	628.1	328.8	709.0
Sterna hirundo	29	1969	2006	14.208	0.402	0.031	3.047	0.094	0.628	14.531	77.90	525.7	112.7	537.6
Sterna nilotica	20	1973	2006	19.668	0.377	0.102	18.525	0.371	0.107	27.018	46.71	649.0	611.3	891.6
Sterna paradisaea	18	1974	2005	61.286	0.740	0.000	23.964	0.492	0.038	65.805	68.64	1899.9	742.9	2039.9
Streptopelia turtur	16	1974	2005	0.709	0.018	0.948	-0.407	-0.010	0.970	0.818	330.15	22.0	-12.6	25.4
Sylvia borin	13	1985	2006				0.478	0.127	0.680	0.478	0.00	0.0	10.0	10.0
Tringa glareola	25	1978	2006	5.684	0.152	0.470	-5.016	-0.152	0.477	7.581	318.58	159.2	-140.4	212.3
Tringa nebularia	30	1969	2006	9.736	0.362	0.049	-3.376	-0.115	0.545	10.305	340.87	360.2	-124.9	381.3
Tringa stagnatilis	18	1976	2006	-11.360	-0.518	0.028	7.286	0.231	0.357	13.496	147.33	-340.8	218.6	404.9

PART III/III
Only species with n≥10 are shown

	NORTHERN EDGE						
Species	n	First year	Last year	Slope (km/yr)	r	p	Displacement (km)
Acrocephalus scirpaceus	10	1986	2005	10.254	0.664	0.073	194.8
Anas querquedula	17	1977	2006	2.663	0.087	0.741	77.2
Apus apus	14	1971	2006	5.994	0.462	0.096	209.8
Ardea purpurea	14	1986	2006	-0.089	-0.002	0.994	-1.8
Ardeola ralloides	22	1972	2006	8.192	0.399	0.066	278.5
Calidris ferruginea	15	1982	2006	8.732	0.234	0.401	209.6
Chlidonias hybrida	19	1972	2006	6.313	0.720	0.001	214.7
Chlidonias niger	15	1974	2005	-16.916	-0.478	0.072	-524.4
Ciconia nigra	19	1977	2006	-4.448	-0.161	0.511	-129.0
Circaetus gallicus	12	1976	2006	7.373	0.851	0.004	221.2
Circus pygargus	10	1991	2006	24.32	0.745	0.013	364.8
Clamator glandarius	10	1980	2003	24.853	0.649	0.042	571.6
Delichon urbica	18	1977	2006	16.19	0.622	0.006	469.5
Falco naumanni	18	1972	2006	5.924	0.357	0.145	201.4
Falco subbuteo	12	1982	2004	6.745	0.345	0.272	148.4
Ficedula hypoleuca	11	1977	2006	23.472	0.709	0.022	680.7
Hieraaetus pennatus	24	1976	2006	9.689	0.467	0.021	290.7
Hirundo daurica	10	1990	2006	4.835	0.224	0.563	77.4
Hirundo rustica	23	1978	2006	14.473	0.614	0.002	405.2
Ixobrychus minutus	18	1987	2006	21.616	0.860	0.000	410.7
Milvus migrans	19	1983	2006	15.926	0.809	0.000	366.3
Motacilla flava	21	1977	2006	14.171	0.632	0.002	411.0
Neophron percnopterus	15	1987	2006	15.02	0.317	0.249	285.4
Numenius phaeopus	27	1972	2006	10.931	0.428	0.026	371.7
Nycticorax nycticorax	20	1979	2006	9.949	0.370	0.108	268.6
Otus scops	11	1981	2006	10.173	0.568	0.087	254.3
Pandion haliaetus	24	1975	2006	20.569	0.806	0.000	637.6
Pernis apivorus	11	1987	2006	-7.524	-0.230	0.497	-143.0
Riparia riparia	12	1993	2006	-0.657	-0.017	0.957	-8.5
Sterna hirundo	17	1974	2006	-4.945	-0.160	0.539	-158.2
Sterna paradisaea	12	1977	2005	25.152	0.805	0.002	704.3
Streptopelia turtur	10	1974	2005	-8.8	-0.557	0.119	-272.8
Tringa glareola	21	1978	2006	2.819	0.287	0.234	78.9
Tringa nebularia	25	1974	2006	12.104	0.763	0.000	387.3
Tringa stagnatilis	14	1976	2006	-11.647	-0.537	0.047	-349.4

Extensive Summary

1. Theoretical framework

Recent climate change is altering the migratory behaviour of many bird species. An advancement in the timing of spring events and a shift in the geographical distribution have been detected for birds around the world. In particular, intra-Palearctic migratory birds have advanced arrivals in spring and shortened migratory distances by shifting northward their wintering grounds. These changes in migration are considered adaptive responses facilitating the adjustment of the life-cycle to the phenological changes found in their areas of reproduction. Long-distance migrants and short-distance migrants breeding in the same regions are exposed to the same selective pressures. Yet, while the shortening of migration is well established in short-distance migrants, hitherto no research has systematically studied the potential for shortening migration distance in long-distance migrants. Adaptive capacity is expected to differ between species differing in the control of migratory behaviour, according to the evidences that suggest the inability of long-distance migrant passerines to undertake adaptive changes.
Studies on a population scale could be key to assess the adaptive potential of migratory birds by identifying the factors that contribute to the adjustment of the phenotype to environmental changes.

2. Objectives

The main aim of this thesis is to give new insights on the capacity of migratory birds to adapt to global change. To fulfil this aim, a top-down approach both at a spatial and at a temporal scale was followed, i.e. from regional to local scale and from long- to short-term periods. The first section explores patterns and potential causes of the shortening of migration distance in European trans-Saharan migrants. This large-scale long-term study involved many of the Palearctic migratory species of birds. In particular, the following questions were addressed:

(1) Are long-distance European migrants shortening their migration distance by establishing wintering population north of the Sahara? (Chapters I and II)

(2) Is it possible to identify hot-spots that need higher degree of protection for the increasing phenomenon of wintering of trans-Saharan birds in Europe? (Chapter I)
(3) Have the populations of trans-Saharan species wintering north of the Sahara increased or remained stable in the last decades? (Chapter II and III)
(4) Which ecological features determine the probability of a species to show an adaptive shortening of migration distance? (Chapter II)
(5) Do passerine and non-passerine long-distance migrants differ in their adaptive capacity when facing selection favouring a shortening of migration distance? (Chapter II)
(6) Is the observed shortening of migration distance related to climatic warming in the last decades? (Chapter III)
(7) Are populations that have established wintering quarters in Europe moving their wintering ranges northwards? (Chapter IV)

Given that adaptive processes happen at the population scale, the second section is dedicated to explore individual features that may be affecting selection of migratory behaviour at a local scale. For this purpose, a partially migratory population of Blackcaps from Eastern Spain was studied. Specific questions addressed in this section were:
(1) Is there phenotypic and genetic variation in a life-history trait traditionally considered invariable? (Chapter V)
(2) How strong are selective pressures related to migratory behaviour acting at the morphological level? (Chapter VI)
(3) What are the behavioural consequences of different migratory strategies in a wintering quarter shared by local residents and northern migrants? (Chapter VII)
(4) Do the complex dynamics of coexistence established in wintering areas generate a pattern for which individual differences in key features (e.g. age, sex, body size) are reflected in behavioural differences, ultimately promoting the maintenance of a large variability in migratory behaviour within a single species? (Chapter VII)

3. Methods

The first section is based on a compilation of all published winter observations in the Iberian Peninsula and Morocco of 80 species of European trans-Saharan birds between 1969 and 2006. Firstly, temporal trends in the incidence of this new behaviour, i.e. wintering north of the

Sahara (Chapters I, II, IV), were explored both at specific and at functional group level. In a second step, the species-specific traits relates to the propensity to establish new wintering populations were investigated by the mean of a comparative analyses (Chapter II). To determine whether global warming is related to the observed behavioural change in migration, were then explored the effects of temperatures in breeding, passage and wintering areas during different stages of the life-cycle on the probability of wintering north of the Sahara (Chapter III). Finally, it was explored how recently established wintering populations are colonizing the Iberian Peninsula and whether the shortening of migration is still going on (Chapter IV).

The second section is based on field data collected between 2010 and 2012 on a partially migratory population of Blackcaps from Eastern Spain. Field data along with common-garden experiments were used to assess the genetic basis of an anomalous moult pattern found in this population (Chapter V). Individual recapture histories, morphological analyses and isotopic signatures in feathers and claws were used to study the occurrence of parameters that allow discrimination between birds belonging to the three groups found in the study area (Chapter VI): northern migrants wintering in the area (W), local year-round residents (R) and local breeders that migrate away in winter (M). Finally, patterns of dominance and habitat use of R and W birds that winter sympatrically were explored by observations of individually-marked birds and radio-telemetry (Chapter VII).

4. Results

The results of this thesis can be summarized in 13 main findings [chapters in bracket]: (1) At least 41 out of the 80 studied species of European trans-Saharan migratory birds have established wintering populations north of the Sahara [I to IV]. (2) In most species, these populations have significantly increased in the last decades [II, III]. (3) Coastal wetlands are hot-spots where most of these new wintering individuals occur [I, II]. (4) Species that have larger wintering ranges in Africa and arrive early in spring to Europe are more likely to establish wintering populations north of the Sahara [II]. (5) Non-passerines showed a stronger adaptive response than passerine species [I to III]. (6) Temperature trends in Europe in the last decades are not related to the incidence of wintering of trans-Saharan migrants north of the Sahara [III]. (7) Once trans-Saharan migrants have established wintering populations north of the Sahara, both the northern limit and the centre of

occurrence of the new wintering range continues to gradually shift northwards [IV]. (8) There is undetected phenotypic and genetic variation in the pattern of juvenile moult of Blackcaps [V]. (9) Resident Blackcaps, which probably descended from a migratory lineage, still have migratory appearance in their flight-related morphology [VI]. (10) Residents and migrants from a partially migratory population do not differ in migration-related plumage morphology [VI]. (11) When sharing a wintering territory, resident Blackcaps are dominant over migrants, despite their smaller body size [VII]. (12) Resident and migratory Blackcaps have differently composed winter home ranges but the same habitat preferences [VII]. (13) The composition of the wintering population suggests the occurrence of sex-biased and environmental-dependent partial migration [VII].

5. Discussion

Results of this thesis provide the first evidence that European trans-Saharan migratory birds have reduced migration distances in last decades. Even if we found no direct relation between this new behaviour and climate warming, it is likely that progressive changes in climatic variables other than temperatures determined the emergence and increase of the wintering north of the Sahara in many European long-distance migrants. Non-passerines and species that traditionally had the largest wintering ranges seem to have the stronger adaptive response: a result that is in accord with the findings of previous studies on the advancement of spring phenology. Cryptic genetic variation in life-history traits may contribute to the potential of some populations of migratory birds to adapt to new selective pressures, as in the case of the genetic variability in the determination of moult pattern in juvenile Blackcaps. However, the lack of differences in plumage morphology between resident and migratory birds of a partially migratory population of Blackcaps, suggest that even in the presence of genetic variation for a particular trait, adaptive changes on “hardware”, as morphological traits, may take long time to occur, if compared to changes in “software”, as migratory behaviour. Dominance relationships clearly emerged between local and wintering Blackcaps, possibly determining the occurrence of partial-migration, given that only few local birds seem able to stand the competition with wintering conspecifics. These complex relationships established during winter may contribute to maintain over evolutionary times the high variability in migratory behaviour observed at the intra-specific as well as at the intra-population levels.

6. Conclusions

6.1 A general reduction in migration distances occurred in European trans-Saharan migrants in the last decades and is still on-going at intra-Palearctic latitudes.

Establishment of wintering populations of many species of long-distance migrants north of the Sahara along the western European flyway emerged from data compiled in this thesis. During the last decades, the number of species and individuals has progressively increased in the new wintering quarters. A northward shift of the new wintering areas is continuing among populations established north of the Sahara. The whole process is consistent with predictions on the adaptive response that may help migratory birds to cope with the new selective regimes imposed by climate change in the northern hemisphere, which are mainly characterized by favouring earlier arrival at the breeding areas.

6.2 Establishment of wintering populations north of the Sahara is more likely for species that have wide wintering ranges and return to their European breeding sites early in the spring.

Species used to winter in a large variety of habitats and migrate back to Europe early in the seasons are possibly pre-adapted to cope with relatively unfavourable conditions both during wintering period and during migration, so that establish wintering populations at northern latitude with greater probability. Given the speed to which global change is occurring, and the rate to which selective pressures for earlier arrival at the breeding quarters are running, only species with flexible migration schedule and great tolerance to environmental conditions may be able to develop the adequate adaptive response, as wintering in the Mediterranean basin in this case.

6.3 Establishment of wintering populations north of the Sahara is generally constrained among passerines species.

The coarse distinction between passerines and non-passerines species remains a very effective tool to describe the lack of adaptive response in a vast number of long-distance migrants, which almost exclusively belong to the order *Passeriformes*. Of course, this difference is thought to reflect differences in the control of migration, considered to be strictly genetic (and less flexible) in most of the passerines, while more environmentally

and social-mediated in non-passerines. The review of the few passerines species that established wintering populations north of the Sahara confirmed this hypothesis, given that they all migrate in groups and have highly social habits.

6.4 Recent temperature trends in Europe are not linked with the establishment of long-distance migrants north of the Sahara.
Changes in other climatic variables, as well as in land use may have played a major role in improving the suitability of north-Saharan regions as new wintering quarters for trans-Saharan migrants. At the same time, worsening of ecological conditions in traditional wintering quarters probably contributed to reinforce selection favouring shorter migration distances.

6.5 Undetected variation in genetically determined traits occurs in wild bird populations and possibly contributes to their adaptive potential.
Even in a well-studied passerine as the Blackcap, our knowledge of the extent of the factors that fuel adaptive potential is limited, as shown by the occurrence of previously undetected genetic variation in moult patterns. The fact that this was found in two populations differing in migratory habits (fully migrant and partial-migrant), suggest that undetected phenotypic variation may be commonly present in wild bird population. Eventually, this may be regarded as a stock of adaptive genetic variation that is generally hard to detect.

6.6 Changes in flight morphology mediated by natural selection occur at a slower rate than changes in migratory behaviour and do not result in different morphotypes in residents and migrants in a partially migratory population.
Occurrence of “migrant-shaped” resident Blackcaps suggests that populations that presumably became resident recently, need longer time to adapt their morphology to the new behavioural condition. This may indicate that the strength of selection shaping flight morphology is not intense, which is also supported by the fact that residents and migrants of the same breeding population are morphologically indistinguishable. However, if partial migration is environmentally determined, different morphologies would not emerge, given that selective pressures on morphologies would fluctuate on a yearly scale.

6.7 Energetic costs to behave as resident and inability of migrant individuals to gain territories held by residents contribute to maintain the great variability of migratory habits in the Blackcap.

In sympatric wintering grounds, resident birds are involved in aggressive interactions with migratory conspecifics and maintain home-ranges with more varied habitats, although they use the same resources as migrants, which settle in home-ranges that better reflect winter needs. For local breeders, maintaining their territory throughout the year may be advantageous in terms of fitness. However, this behaviour is energetically costly and only some birds, adult males in particular, may be in the condition to undertake it. Together, these factors probably contribute to maintain the wide variety of migratory habits observed in Blackcaps. Given that variability fuels adaptive potential, these mechanisms ultimately maintain high the potential for population of this species to cope with climate change.

Amplio Resumen

El potencial de las aves para adaptarse al cambio climático: lecciones de las aves europeas migratorias de larga distancia y de las Currucas Capirotadas (*Sylvia atricapilla*) ibéricas

1. Marco teórico

El reciente cambio climático está alterando el comportamiento migratorio de muchas especies de aves. Se han detectado adelantos de la fenología primaveral y cambios en la distribución geográfica en especies de aves de todo el mundo. Más concretamente, se ha visto que las aves migratorias intra-paleárticas han adelantado su llegada primaveral a los cuarteles de cría y han acortado su distancia de migración gracias al desplazamiento hacia el norte de sus áreas de invernada. Estos cambios en los patrones migratorios se han interpretado como respuestas adaptativas que facilitarían el ajuste del ciclo de vida de estas aves a los cambios fenológicos que ocurren en sus áreas de reproducción. Los migrantes de larga y corta distancia que se reproducen en las mismas regiones están expuestos a las mismas presiones selectivas durante la época reproductiva. Sin embargo, mientras que la reducción de la distancia de migración está ampliamente descrita en la bibliografía para los migrantes de corta distancia, hasta el momento no se ha estudiado sistemáticamente el potencial que tienen los migrantes de larga distancia de acortar sus distancias migratorias. Cabe esperar que la capacidad de adaptación difiera entre especies con diferentes tipos de control del comportamiento migratorio, como lo demuestran las evidencias que sugieren una incapacidad de los paseriformes migrantes de larga-distancia para efectuar cambios adaptativos. Estudios a nivel poblacional podrían ser claves para entender el potencial de adaptación de las aves migratorias, al identificar los factores que contribuyen a potenciar la capacidad adaptativa de estas aves.

2. Objetivos

El objetivo principal de esta tesis es investigar la capacidad adaptativa de las aves migratorias frente al cambio global. Para alcanzarlo, se ha seguido,

tanto a escala espacial como temporal, un enfoque *top-down*: empecé explorando patrones a macroescala (península ibérica y Marruecos) y a largo plazo (cuatro décadas), para luego aplicar una aproximación a microescala (sobre una población concreta) y a corto plazo (tres años). En la primera sección, investigué si la distancia de migración en 80 especies de aves trans-Saharianas europeas ha mostrado una reducción a lo largo del tiempo y cuales han podido ser sus causas mediante una serie de preguntas sucesivas:

(1) ¿Los migrantes de larga distancia han acortado su distancia de migración mediante el establecimiento de poblaciones invernantes al norte del Sahara? (Capítulos I y II)
(2) ¿Es posible identificar áreas naturales especialmente favorables para el fenómeno creciente de la invernada de las aves transaharianas en Europa y que, por tanto, requieran un mayor grado de protección? (Capítulo I)
(3) ¿Las poblaciones de aves transaharianas que se han establecido al norte del Sahara han aumentado o se ha mantenido estables en las últimas décadas? (Capítulos II y III)
(4) ¿Qué características biológicas determinan la probabilidad de que una especie muestre una reducción adaptativa de la distancia de migración? (Capítulo II)
(5) ¿Paseriformes y no paseriformes difieren en su capacidad de adaptación frente a la selección que favorece una reducción de la distancia de la migración? (Capítulo II)
(6) ¿El acortamiento de la distancia de migración está relacionado con el incremento de temperaturas registrado en las últimas décadas? (Capítulo III)
(7) ¿Las poblaciones que han logrado establecer cuarteles de invernada en Europa, siguen desplazando sus áreas de invernada hacia el norte? (Capítulo IV)

Dado que los procesos adaptativos ocurren a escala poblacional, la segunda sección de la tesis la he dedicado a explorar las características individuales que pueden estar afectando la selección del comportamiento migratorio a escala local. Con este fin, he estudiado una población parcialmente migratoria de Currucas Capirotadas del levante español. Las preguntas abordadas en esta sección son:
(1) ¿Existe variación fenotípica y genética en un rasgo del ciclo vital tradicionalmente considerado invariable? (Capítulo V)

(2) ¿Cómo de fuertes son las presiones selectivas que actúan a nivel morfológico relacionadas con el comportamiento migratorio? (Capítulo VI)
(3) ¿Cuáles son las consecuencias comportamentales de diferentes estrategias migratorias en un cuartel de invernada compartido por individuos residentes locales y migrantes del norte de Europa? (Capítulo VII)
(4) ¿Las complejas dinámicas de convivencia establecidas en las zonas de invernada generan un patrón para el que diferencias en características individuales (como edad, sexo o tamaño corporal) se reflejan en diferencias comportamentales, promoviendo en última instancia el mantenimiento de una gran variabilidad en el comportamiento migratorio dentro una sola especie? (Capítulo VII)

3. Métodos

La primera sección se basa en una recopilación de todas las observaciones publicadas de ejemplares de 80 especies de aves transaharianas europeas registrados en invierno en la península ibérica y Marruecos entre 1969 y 2006. En primer lugar, he explorado las tendencias temporales de la incidencia de este nuevo comportamiento de invernada al norte del Sahara (Capítulos I, II, III), tanto especie por especie como por grupos funcionales (paseriformes vs no paseriformes). En segundo lugar, he investigado los rasgos específicos asociados con la tendencia a establecer nuevas poblaciones invernantes a través de un análisis comparativo (Capítulo II). Para determinar si el calentamiento global está relacionado con el cambio observado en el comportamiento migratorio, también exploré si las temperaturas en las áreas de nidificación, paso post-nupcial e invernada durante diferentes etapas del ciclo vital estaban asociadas con la probabilidad de invernar al norte del Sahara (Capítulo III). Finalmente, investigué cómo están colonizando la península ibérica las poblaciones invernantes recién establecidas y si, por tanto, en estas poblaciones se sigue reduciendo la migración (Capítulo IV).
La segunda sección se basa en datos de campo empíricos tomados entre 2010 y 2012 en una población parcialmente migratoria de Currucas Capirotadas del este de España. Parte de estos datos de campo, junto con las evidencias proporcionadas por experimentos de tipo *"common-garden"*, sirvieron para evaluar la base genética de un patrón de muda anómalo encontrado en la población estudiada (Capítulo V). Los historiales individuales de recapturas, junto con análisis morfológicos y los perfiles

isotópicos de plumas y uñas se usaron para estudiar que parámetros permitían discriminar de manera más certera de las aves pertenecientes a los tres grupos de Currucas Capirotadas que se encuentran en el área de estudio (Capítulo VI): inmigrantes del norte que invernan en el área (W), residentes durante todo el año (R), y los que crían en el área pero que la abandonan durante el invierno (M). Finalmente, los patrones de dominancia y el uso del hábitat de las aves W y R que invernan simpátricamente se estudiaron mediante observaciones etológicas de aves marcadas y radio-seguimiento (Capítulo VII).

4. Resultados

Los resultados principales pueden resumirse en los siguientes puntos [entre corchetes los capítulos donde aparecen]: (1) Por lo menos 41 de las 80 especies de aves migratorias transaharianas Europeas estudiadas han establecido poblaciones invernantes al norte del Sahara [I a IV]. (2) En la mayoría de las especies, estas nuevas poblaciones invernantes, además, han incrementado sus efectivos de forma significativa en las últimas décadas [II, III]. (3) Los humedales costeros concentran la mayoría de observaciones de individuos invernantes, por lo que parecen ser zonas importantes para estas nuevas poblaciones [I, II]. (4) Las especies que tienen áreas de invernada africanas más extensas y que llegan a Europa más pronto en primavera tienen más probabilidades de establecer poblaciones invernantes al norte del Sahara [II]. (5) Las especies de no-paseriformes mostraron una respuesta adaptativa más fuerte que los paseriformes [I a III]. (6) Los patrones de temperaturas registrados en Europa en las últimas décadas no están relacionado con la incidencia de la invernada de migrantes transaharianos al norte del Sahara [III]. (7) Una vez que especies de migrantes transaharianas establecen poblaciones invernantes al norte del Sahara, tanto el límite norte como el baricentro de sus nuevas áreas de invernada siguen desplazándose gradualmente hacia el norte [IV]. (8) Existe una varianza fenotípica y genotípica previamente no detectada en el patrón de muda juvenil de la Curruca Capirotada [V]. (9) Las Currucas Capirotadas residentes, que probablemente descienden de un linaje migratorio, todavía tienen la morfología del plumaje propia de migradores [VI]. (10) Residentes y migrantes en la población parcialmente migratoria de Currucas Capirotadas estudiada no difirieron en la morfología de su plumaje [VI]. (11) En territorios de invernada compartidos, las

Currucas Capirotadas residentes son dominantes sobre las migrantes, a pesar de tener un menor tamaño corporal [VII]. (12) El hábitat de las áreas de campeo de invierno difirió en su composición entre individuos residentes y migrantes, si bien, ambos, mostraron las mismas preferencias por ciertos tipos de hábitat [VII]. (13) La composición de la población en invierno sugiere la existencia de migración parcial mediada por el sexo de los individuos y muy dependiente de las condiciones medioambientales [VII].

5. Discusión

Esta tesis proporciona las primeras evidencias de que las aves migratorias transaharianas europeas han reducido sus distancias de migración a lo largo de las últimas décadas mediante el establecimiento de nuevas áreas de invernada en la región mediterránea. Aunque no se pudo encontrar una relación entre este cambio comportamental y el clima, sigue siendo plausible que cambios en otras variables -diferentes a la temperatura- estén detrás del fenómeno observado. Las especies de no paseriformes, las que tradicionalmente tenían unas áreas de invernada más extensas, y las que volvían más pronto en primavera parecen mostrar la respuesta adaptativa más fuerte. Este resultado concuerda con los hallazgos de estudios previos sobre los patrones de adelanto de la fenología primaveral.

Una cierta variación genética críptica en los rasgos del ciclo vital puede favorecer la capacidad de adaptación de algunas poblaciones de aves migratorias a las nuevas presiones selectivas, como es el caso de la variabilidad genética en la determinación del patrón de muda en los juveniles de Curruca Capirotada. Sin embargo, la ausencia de diferencias en la morfología del plumaje en aves residentes y migrantes, sugiere que incluso en presencia de variación genética en la determinación de un rasgo especifico, los cambios adaptativos en el "*hardware*", como son los rasgos morfológicos, pueden tardar mucho tiempo en producirse, sobre todo comparado con el tiempo requerido para cambios en el "*software*", como puede ser el comportamiento migratorio.

Parecen existir claramente relaciones de dominancia entre Currucas Capirotadas locales e invernantes, lo que posiblemente determina la existencia de un patrón de migración parcial en la población reproductora local, ya que sólo algunas de las aves locales parecen ser capaces de aguantar la competencia de sus congéneres invernantes. Estas complejas

relaciones establecidas durante el invierno puede que contribuyan a mantener a lo largo de tiempos evolutivos la alta variabilidad en el comportamiento migratorio observado a nivel intra-específico, así como intra-poblacional en la Curruca Capirotada.

6. Conclusiones

6.1 Se produjo una reducción general de las distancias de migración en los migrantes trans-Saharianos Europeos a lo largo de las últimas décadas, reducción que está todavía en curso en latitudes intra-Paleárticas.

Se deduce claramente, por los datos presentados en esta tesis, que existe un establecimiento de poblaciones invernantes al norte del Sahara de muchas especies de aves migrantes de larga distancia a lo largo de la ruta migratoria de Europa occidental. A lo largo de las últimas décadas, tanto el número de especies como el de individuos en los nuevos cuarteles de invernada ha aumentado progresivamente. El desplazamiento hacia el norte de las nuevas áreas de invernada continúa en las poblaciones ya establecidas al norte del Sahara. Este proceso es consistente con las predicciones teóricas sobre la respuesta adaptativa de las aves migratorias frente a los nuevos regímenes de selección impuestos por el cambio climático en el hemisferio norte, los cuales se caracterizan principalmente por favorecer una llegada más temprana a las zonas de cría.

6.2 El establecimiento de poblaciones invernantes al norte del Sahara es más probable en las especies que tienen el área de invernada más extensa y una fecha de retorno en primavera a Europa más temprana.

Las especies que suelen pasar el invierno en una gran variedad de hábitats y migrar a Europa a principios de la temporada primaveral parecen estar pre-adaptadas para hacer frente a condiciones relativamente desfavorables, tanto durante la invernada como durante el período de migración, por lo que han podido establecer poblaciones invernantes con mayor probabilidad. Dada la velocidad a la que se está produciendo el cambio global y la tasa a la que están actuando las presiones selectivas que favorecen las llegadas más tempranas a los cuarteles de reproducción, solamente aquellas especies con una fenología migratoria más flexible y una gran tolerancia a las condiciones ambientales pueden ser capaces de desarrollar una respuesta adaptativa adecuada, como en este caso la invernada en la cuenca Mediterránea.

6.3 El establecimiento de poblaciones invernantes al norte del Sahara es infrecuente entre las especies de paseriformes.

Aunque meramente funcional, la distinción entre las especies paseriformes y las que no lo son es una herramienta muy eficaz para determinar la probabilidad de que haya una respuesta adaptativa, ya que las especies que no mostraron cambios pertenecieron casi exclusivamente al orden *Passeriformes*. Esta distinción debe reflejar diferencias sustanciales en el control de la migración. Éste tiene una base genética inflexible en la mayoría de paseriformes, mientras que en los no paseriformes está principalmente determinado por influencias ambientales y sociales. Está hipótesis se ve confirmada al comprobar que las pocas especies de paseriformes invernantes que pudieron establecer poblaciones invernantes tienen hábitos muy sociales y migran en grupos.

6.4 Las recientes tendencias de las temperaturas en Europa no predicen el establecimiento de migrantes de larga distancia al norte del Sahara.

Los cambios en otras variables climáticas, así como los cambios en los usos del suelo pueden haber desempeñado un papel importante a la hora de mejorar la idoneidad de las regiones al norte del Sahara como zonas de invernada para los migrantes transaharianos. Simultáneamente, el empeoramiento de las condiciones ecológicas en los cuarteles de invernada tradicionales en el África subsahariana también contribuyó probablemente a reforzar la selección a favor de una reducción de la distancia de migración.

6.5 Existe cierta variabilidad fenotípica incluso en los rasgos bajo un estricto control genético, que contribuye a fomentar el potencial adaptativo de las poblaciones de aves silvestres.

Incluso en un paseriforme bien estudiado, como es la Curruca Capirotada, sabemos muy poco acerca de los factores que fomentan el potencial adaptativo, como lo demuestra el hallazgo de una variación fenotípica con base genética nunca antes descrita en los patrones de muda de esta especie. El hecho de que esta variabilidad fuera encontrada en dos poblaciones con diferentes comportamientos migratorios (una total y otra parcialmente migratoria), sugiere que este tipo de variación fenotípica no detectada podría estar presente en muchas poblaciones de aves silvestres de manera habitual. Esta variabilidad puede considerarse como una reserva de variación genética adaptativa generalmente difícil de detectar.

6.6 Los cambios en la morfología de vuelo mediados por selección natural se producen a un ritmo más lento que los cambios en el comportamiento migratorio y no dan lugar a diferentes morfotipos entre residentes y migrantes de una población parcialmente migratoria.

La existencia de Currucas Capirotadas residentes con una morfología típica de las poblaciones migratorias sugiere que las poblaciones, que han desarrollado en tiempos recientes su condición sedentaria, necesitan un plazo de tiempo aún más largo para adaptar su morfología a su nueva condición comportamental. Esto puede indicar que las presiones de selección que moldean la morfología de vuelo no son intensas, como también apoya el hecho de que residentes y migrantes de la misma población reproductora sean morfológicamente indistinguibles. Sin embargo, si la condición de migración parcial está primariamente determinada por las condiciones ambientales, no hay posibilidades de que surjan diferentes morfologías, dado que las presiones selectivas que actúan a nivel morfológico fluctuarán a lo largo del tiempo.

6.7 Los costes energéticos asociados a la condición residente, así como la incapacidad de los migrantes de ocupar los territorios de los residentes, contribuyen a mantener la gran variabilidad de los hábitos migratorios observados en la Curruca Capirotada.

En áreas de invernada comunes, las aves residentes se ven involucradas en interacciones agresivas con sus congéneres migrantes y mantienen unas áreas de campeo compuestas por una mayor diversidad de hábitats. No obstante, dentro de sus áreas de campeo, los residentes utilizan los mismos recursos que los migrantes, los cuales se instalan en áreas de campeo más acordes con las necesidades invernales. Para los residentes que se reproducen en la misma área, el mantenimiento de un territorio proprio a lo largo de todo el año puede conferir ventajas en términos de éxito reproductor. Sin embargo, este comportamiento es energéticamente costoso y sólo algunas aves, especialmente los machos adultos, están en condiciones de llevarlo a cabo. En conjunto, estos factores probablemente contribuyen a mantener la amplia variedad de hábitos migratorios observados en la Curruca Capirotada. Dado que la variabilidad es el principal requerimiento para el potencial adaptativo de las especies, estos mecanismos ayudarían, en última instancia, a mantener alta en las poblaciones de esta especie la capacidad de afrontar el cambio climático.

References

Adamik P and Pietruszková J. 2008. Advances in spring but variable autumnal trends in timing of inland wader migration. Acta Ornithologica 43 (2): 119-128.

Adriaensen F and Dhondt A. 1990. Population dynamics and partial migration of the European robin (Erithacus rubecula) in different habitats. Journal of Animal Ecology 59: 1077–1090.

Adriaensen F, Ulenaers P and Dhondt AA. 1993. Ringing recoveries and the increase in numbers of European great crested grebes Podiceps cristatus. Ardea 81: 59–70.

Ahola MP, Laaksonen T, Sippola K, Eeva T, Rainio K and Lehikoinen E. 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. Global Change Biology 10: 1610–1617.

Ahola MP, Laaksonen T, Eeva T and Lehikoninen E. 2009. Great tits lay increasingly smaller clutches than selected for: a study of climate- and density-related changes in reproductive traits. Journal of Animal Ecology 76: 1045-1052.

Akaike H. 1973. Information theory and an extension of the maximum likelihood principle. In Petrov BN and Csaki F (Eds.), Second international symposium on information theory (pp. 267281). Budapest: Academiai Kiado.

Alerstam T, Hake M and Kjellén N. 2006. Temporal and spatial patterns of repeated migratory journeys by ospreys. Animal Behaviour 71: 555-566.

Alerstam T, Hedenstrom A and Akesson S. 2003. Long-distance migration: evolution and determinants. Oikos 103: 247-260.

Ambrosini R, Rubolini D, Møller A, Bani L, Clark J, Karcza Z, Vangeluwe D, du Feu C, Spina F and Saino N. 2011. Climate change and the long-term northward shift in the African wintering range of the barn swallow Hirundo rustica. Climate Research 49: 131–141.

Anyamba A and Tucker CJ. 2005. Analysis of Sahelian vegetation dynamics using NOAA-AVHRR NDVI data from 1981-2003. Journal of Arid Environments 63: 596-614.

Arizaga J, Barba E, Cantó JL, Cívico JM, Cortés V, Greño JL, Herranz JM, Monrós JS, Moreno P, Piculo R and Verdejo J. 2012. The usefulness of biometrics for the study of avian connectivity within Europe. A case study with Blackcaps Sylvia atricapilla in Spain. Ardeola 59(1): 75-91.

Assandri G, Morganti M, Bogliani G and Pulido F. 2013. Selezione dell'habitat nel ciclo annuale in una popolazione spagnola di Capinere Sylvia atricapilla: l'importanza della coltivazione non intensiva degli uliveti. XVII Convegno Italiano di Ornitologia, Trento, Italy.

Austin EG and Rehfisch MM. 2005. Shifting non breeding distributions of migratory fauna in relation to climatic change. Global Change Biology 11: 31-38.

Avilova K V and Eremkin GS. 2001. Waterfowl wintering in Moscow (1985-1999): dependence on air temperatures and the prosperity of the human population. Acta Ornitologica 35: 65–71.

Bai ML, Severinghaus LL and Philippart MT. 2012. Mechanisms underlying small-scale partial migration of a subtropical owl. Behavioral Ecology 23(1): 153-159.

Balanya J, Oller JM, Huey RB, Gilchrist GW and Serra L. 2006. Global genetic change tracks global climate warming in Drosophila subobscura. Science 313: 1773–5.

Barbet-Massin M, Walther BA Thuiller W, Rahbek C and Jiguet F. 2009. Potential impacts of climate change on the winter distribution of Afro-Palaearctic migrant passerines. Biology Letters 5: 248–251.

Barluenga M, Barbosa A, Moreno E. 2000. Social relationships due to sex, age and morphology in Great tits Parus major wintering in a mountainous habitat of central Spain. Ardeola 47: 19 – 27.

Barluenga M, Barbosa A, Moreno E. 2000. Social relationships due to sex, age and morphology in Great tits Perus major wintering in a mountainous habitat of central Spain. Ardeola 47: 19 – 27.

Barta Z, Houston AI, McNamara JM, Welham RK, Hedenström A, Weber TP and Feró O. 2006. Annual routines of non-migratory birds: optimal moult strategies. Oikos 112: 580-593.

Barta Z, McNamara JM, Houston AI, Weber TP, Hedenström A, and Feró O. 2008. Optimal moult strategies in migratory birds. Philosophical Transactions of the Royal Society of London B, 363: 211-229.

Bearhop S, Fiedler W, Furness RW, Votier SC, Waldron S, Newton J, Bowen GJ, Berthold P and Farnsworth K. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. Science 310: 502–504.

Bearhop S, Furness RW, Hilton GM, Votier SC, Waldron S. 2003. A forensic approach to understanding diet and habitat use from stable isotope analysis of (avian) claw material. Functional Ecology 17: 270-275.

Beaugrand JP, Payette D and Goulet C. 1995. Conflict outcome in male green swordtail fish dyads (Xiphophorus helleri): interaction of body size, prior dominance/subordination experience and prior residency. Behaviour 133(3/4): 303-319.

Belda EJ, Barba E and Monrós JS. 2007. Resident and transient dynamics, site fidelity and survival in wintering Blackcaps Sylvia atricapilla: evidence from capture-recapture analyses. Ibis 149: 396-404.

Bell CP. 2000. Process in the evolution of bird migration and pattern in avian ecogeography. Journal of Avian Biology 31: 258–265.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W and Courchamp F. Impacts of climate change on future biodiversity. Ecology Letters 15: 365-377.

Berggren Å, Armstrlng DP and Lewis RM. 2004. Delayed plumage maturation increases overwinter survival in North Island robins. Proceedings of the Royal Society of London B 271: 2123–2130.

Bernis F. 1980. La migración de las aves en el estrecho de Gibraltar. Vol. 1. Avesplaneadoras. Universidad Complutense de Madrid. Madrid.

Berthold P and Helbig AJ. 2008. The genetics of bird migration: stimulus, timing and direction. Ibis 134(1): 35-40.

Berthold P and Querner U. 1981. Genetic basis of migratory behaviour in European Warbler. Science 212(4490): 77-79.

Berthold P, Fiedler W, Raim A and Querner U. 1998. 25-year study of the population development of central European songbirds: a general decline, most evident in long-distance migrants. Naturwissenschaften 85: 350-353.

Berthold P, Helbig AJ, Mohr G and Querner U. 1992. Rapid microevolution of migratory behaviour in a wild bird species. Nature 360: 668-670.

Berthold P, Querner U and Mohr G. 1994. Vererbung einer populationsspezifischen Mauser bei Kreuzung von Mönchsgrasmücken (Sylvia atricapilla) verschiedener Populationen. Journal of Ornithology 135: 233-236.

Berthold P, Querner U and Schlenker R. 1990. Die Mönchsgrasmücke. Neue Brehm-Bücherei Nr. 603. Ziemsen, Wittenberg Lutherstadt.

Berthold P, van den Bossche W, Jakubiec Z, Kaatz M and Querner U. 2002. Long-term satellite tracking sheds light upon variable migration strategies of White Storks (Ciconia ciconia). Journal für Ornithologie 143: 489-493.

Berthold P, Wiltschko W, Miltenberg H and Querner U. 1990. Genetic transmission of migratory behaviour into a nonmigratory bird population. Experientia 46(1): 107-108.

Berthold P. 1986. Wintering in a partially migratory Mediterranean Blackcap (Sylvia atricapilla) population: strategy, control, and unanswered questions. Supplemento alle Ricerche Biologia della Selvaggina X. I.N.F.S., Ozzano (BO), Italy.

Berthold P. 1996. Control of bird migration. London, Chapman & Hall.

Berthold P. 1998. Vogelwelt und Klima: gegenwärtige Veränderungen. Naturwiss Rundsch 51: 337–346.

Berthold P. 1999. A comprehensive theory for the evolution, control and adaptability of avian migration. Ostrich 70(1): 1-11.

Berthold P. 2001. Bird migration. A general survey. Oxford University Press.Oxford.

Berthold P. 2002. Bird migration: the present view of evolution, control, and further development as global warming progresses. Acta Zoologica Sinica 48: 291-301.

Berthold P and Querner U. 1982. Genetic basis of moult, wing length, and body weight in a migratory bird species, Sylvia atricapilla. Experientia 38: 801-802.

Bêty J, Giroux JF and Gauthier G. 2004. Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (Anser caerulescens atlanticus). Behavioral Ecology and Sociobiology 57: 1-8.

Bingham RL and Brennan LA. 2004. Comparison of Type I error rates for statistical analyses of resource selection. Journal of Wildlife Management 68: 206-212.

BirdLife International. 2004. Birds in the European Union: a status assessment. Wageningen, The Netherlands: BirdLife International.

Blanco G. 1996. Population dynamics and communal roosting of White Storks foraging at a Spanish refuse dump. Colonial Waterbirds 19: 273-276.

Blasco-Zumeta J. 2012. Atlas de Identificación de las Aves de Aragón http://www.ibercajalav.net/recursos.php?codopcion=2251&codopcion2=2481&codopcion3=2481. Accessed: 1 March 2012.

Bojarinova JG, Lehikoinen E and Eeva T. 1999. Dependence of postjuvenile moult on hatching date, condition and sex in the Great Tit. Journal of Avian Biology 30: 437-446.

Both C and te Marvelde L. 2007. Climate change and timing of avian breeding and migration throughout Europe. Climate Research 35: 93-105.

Both C and Visser ME. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411: 296-298.

Both C, Artemyev AV, Blaauw B, Cowie RJ. Dekhuijzen AJ, Eeva T, Enemar A, Gustafsoon L, Ivankina EV, Järvien A, Metcalfe NB, Nyholm NEI, Potti J, Ravussin PA, Sanz JJ, Silverin B, Slater FM, Sokolov LV, Török J, Winkel W, Wright J, Zang H and Visser ME. 2004. Large–scale geographical variation confirms that climate change causes birds to lay earlier. Proceedings of the Royal Society of London B 271(1549): 1657-1662.

Both C, Bouwhuis S, Lessells CM and Visser ME. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441: 81-83.

Both C, Van Asch M, Bijlsma RG, Van Den Burg AB and Visser ME. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? Journal of Animal Ecology 78: 73-83.

Boyle A. 2008. Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. Journal of Animal Ecology 77(6): 1122-1128.

Brown JH and Maurer BA. 1986. Body size, ecological dominance and Cope's rule. Nature: 324: 248-250.

Bruderer B and Salewski V. 2008. Evolution of bird migration in a biogeographical context. Journal of Biogeography. 35(11): 1951-1959.

Butler MW and McGraw KJ. 2009. Indoor housing during development affects moult, carotenoid circulation and beak colouration of mallard ducks (Anas platyrhynchos). Avian Biology Research 2(4): 203-211.

Camiña A and Montelío E. 2005. Evolución estacional de las aves no paseriformes asociadas al vertedero de RSU de Nájera. Zubía 23: 7-22.

Cantos FJ. 1995. Migración e invernada de la curruca capirotada (Sylvia atricapilla) en la península ibérica. Ecología 9: 425-433.

Catry P, Lecoq M, Conway G, Felgueiras M, King JMB and Hamidi S. 2006. Are Blackcaps Sylvia atricapilla diffrential distance migrants by sex? Ardeola 53(1): 31-38.

Chapman BB, Brönmark C, Nilsson J-Å and Hansson L-A. 2011. The ecology and evolution of partial migration. Oikos 120: 1764–1775.

Chen I, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid Range Shifts of Species of Climate Warming. Science 333: 1024–1026.

Chernestov N, Berthold P and Querner U. 2004. Migratory orientation of first-year white storks (Ciconia ciconia): inherited information and social interactions. Journal of Experimental Biology 207: 937-943.

Cieslak M and Kwiecinski Z. 2009. Moult and breeding of captive Northern Hawk Surnia ulula. Ardea 97(4): 571-579.

Coppack T and Both C. 2002. Predicting life-cycle adaptation of migratory birds to global climate change. Ardea 90: 369-377.

Coppack T and Pulido F. 2004. Photoperiodic response and the adaptability of avian life cycles to environmental change. Advances in Ecological Research 35: 131-150.

Coppack T, Pulido F, Czisch M, Auer DP and Berthold P. 2003. Photoperiodic response may facilitate adaptation to climate change in long-distance migratory birds. Proceedings of the Royal Society of London B 270: 43-45.

Coppack T, Tindemans I, Czisch M, van der Linden A, Berthold P and Pulido F. 2008. Can long-distance migratory birds adjust to the advancement of spring by shortening migration distance? The response of the pied flycatcher to latitudinal photoperiodic variation. Global Change Biology 14: 2516-2522.

Cox GW. 2010. Bird migration and global change. Island Press. Washington.

Cramp S (ed), 1992. Handbook of the birds of Europe, the Middle East and North Africa – The birds of Western Palearctic. Volume VI: Warblers. Oxford: Oxford University Press.

Cramp S (ed). 1977- 1994. Handbook of the birds of Europe, the Middle East and North Africa – The birds of Western Palearctic. Oxford: Oxford University Press.

Cramp S and Simmons KEL (Eds.). 1998. The complete birds of the WesternPalearctic. BWP on CD-ROM. Oxford University Press. Oxford.

Crawley MJ. 1993. GLIM for Ecologists. Blackwell Scientific Publications, Oxford.

Crick HQP and Sparks TH. 1999. Climate change related to egg-laying trends. Nature 399: 423-424.

Cristol DA, Val Nolan Jr and Ketterson ED. 1990. Effect of prior residence on dominance status of dark-eyed juncos, Junco hyemalis. Animal Behaviour 40(3): 580-586.

David HA. 1987. Ranking from unbalanced paired-comparison data. Biometrika 74: 432-436

De Giacomo U and Guerrieri G. 2008. The feeding behavior of the black kite (Milvus migrans) in the rubbish dump of Rome. Journal of Raptor Research. 42(2): 110-118.

de La Hera I, Pérez-Tris J and Tellería JL. 2007. Testing the validity of discriminant function analyses based on bird morphology: the case of migratory and sedentary blackcaps Sylvia atricapilla wintering in southern Iberia. Ardeola 54(1): 81–91.

de la Hera I, Pérez-Tris J and Tellería JL. 2012. Habitat distribution of migratory and sedentary blackcaps Sylvia atricapilla wintering in southern Iberia: a morphological and biogeochemical approach. Journal of Avian Biology 43: 333–340

de la Hera I, Reed TE, Pulido F and Visser ME. 2013 Feather mass and winter moult extent are heritable but not associated with fitness-related traits in a long-distance migratory bird. Evolutionary Ecology 27(6): 1199-1216.

de la Hera I, Schaper SV, Diaz JA, Pérez-Tris J, Bensch S and Tellería JL. 2011. How much variation in the moult duration of passerines can be explained by the growth rate of tail feathers? The Auk 128(2): 321-329.

de Los Santos MR, Cuadrado M and Arjona S. 1986. Variation in the abundance of Blackcaps (Sylvia atricapilla) wintering in an olive (Olea europaea) orchard in southern Spain. Bird study 33: 81-86.

De Vries H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Animal Behaviour 55: 827-843.

Dhondt AA. 1983. Variation in the number of overwintering stonechats possibly caused by natural selection. Ringing & Migration 4: 155–158.

Dickinson JL, Zuckerberg B and Bonter DN. 2010. Citizen science as an ecological research tool. Annual Review of Ecology Evolution and Systematics 41: 149-172.

Dingle H and Drake AV. 2007. What is migration? Bioscience 57(2): 113-121.

Doi H, Gordo O and Katano I. 2008. Heterogeneous intra-annual climatic changes drive different phenological responses at two trophic levels. Climate Research 36: 181-190.

Donázar JA. 1992. Muladares y basureros en la biología y conservación de las aves en España. Ardeola 39: 29-40.

Doswald N, Willis SG, Collingham YC, Pain DJ, Green RE and Huntley B. 2009. Potential impacts of climatic change on the breeding and non-breeding ranges and migration distances of European Sylvia warblers. Journal of Biogeography 36: 1194-1208.

Duriez O, Ens BJ, Choquet R, Pradel R and Klaassen M. 2012. Comparing the seasonal survival of resident and migratory oystercatchers: carry-over effects of habitat quality and weather conditions. Oikos 121: 862-873.

Dyrcz A and Halupka L. 2009. The response of the Great Reed Warbler Acrocephalus arundinaceus to climate change. Journal of Ornithology 150: 39-44.

Egevang C, Stenhouse IJ, Phillips R A, Petersen A, Fox JW and Silk JRD. 2009. Tracking of Arctic terns Sterna paradise reveals longest animal migration. Proceedings of the National Academy of Science 107(5): 2078-2081.

Eichhorn G, Drent RH, Stahl J, Leito A and Alerstam T. 2009. Skipping the Baltic: the emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese. Journal of Animal Ecology 78: 63-72.

Elo AE. 1978. The Rating of Chess Players, Past and Present. New York: Arco.

Erni B, Liechti F and Bruederer B. 2005. The role of wind in passerines autumn migration between Europe and Africa. Behavioural Ecology 16: 733-739.

Evans KL, Newton J, Gaston KJ, Sharp SP, McGowan A and Hatchwell BJ. 2012. Colonisation of urban environments is associated with reduced migratory behaviour, facilitating divergence from ancestral populations. Oikos 121: 634–640.

Falconer DS and Mackay TFC. 1996. Introduction to quantitative genetics. Essex: Longman Scientific & Technical.

Fasola M and Ruiz X. 1996. The value of rice fields as substitutes for natural wetlands for waterbirds in the Mediterranean region. Colonial Waterbirds 19: 122-128.

Fasola M, Rubolini D, Merli E, Boncompagni E and Bressan U. 2010. Long-term trends of heron and egret populations in Italy, and the effects of climate, human-induced mortality, and habitat on population dynamics. Population Ecology 52: 59-76.

Felsenstein J. 1985. Phylogenies and the comparative method. The American Naturalist 125(1): 1-15.

Fiedler W, Bairlein F and Koppen U. 2004. Using large-scale data from ringed birds for the investigation of effects of climate change on migrating birds: pitfalls and prospects. Advances in Ecological Research 35: 49–67.

Fiedler W. 2001. Large-scale ringing recovery analysis of European white storks (Ciconia ciconia). Ring 23: 73-79.

Fiedler W. 2003. Recent changes in migratory behaviour of birds: a compilation of field observations and ringing data. In: Berthold P, Gwinner E, Sonnenschein E, editors. Avian migration. Heidelberg: Springer. p 21-38.

Fiedler W. 2005. Ecomorphology of the external flight apparatus of blackcaps (Sylvia atricapilla) with different migration behaviour. Annals of the New York Academy of Science 1046(2005): 253–263.

Finlayson JC. 1992. Birds of the Strait of Gibraltar. Academic Press. T. & A. D.Poyser. London.

Fudickar AM and Partecke J. 2012. The flight apparatus of migratory and sedentary individuals of a partially migratory songbird species. PLoS ONE 7(12): e51920.

Fudickar AM, Schmidt A, Hau M, Quetting M and Partecke J. 2013. Female-biased obligate strategies in a partially migratory population. Journal of Animal Ecology 82(4): 863-871.

Gallego MC, Trigo RM, Vaquero JM, Brunet M, García JA, Sigró J and Valente MA. 2011. Trends in frequency indices of daily precipitation over the Iberian Peninsula during the last century. 116: 1–18.

Gargallo G. and Clarabuch U. 1995. Extensive moult and ageing in six species of passerines. Ringing & Migration, 16: 178-189.

Garrido JR and García Sarasa C. 1998. Importancia del vertedero de Los Barrios (Campo de Gibraltar, Cádiz) en la ruta migratoria occidental del Milano

negro (Milvus migrans) y el buitre leonado (Gyps fulvus). Almoraima 19: 217-224.

Garrido JR, Molina B, Del Moral JC. (eds). 2012. Las garzas en España, población reproductora e invernante en 2010-2011 y método de censo. SEO/Birdlife. Madrid.

Gauci C. and Sultana J. 1979. Moult of the Sardinian Warbler. Il-Merill, 20: 1-13.

Gauthreaux SA. 1978. The ecological significance of behavioral dominance. In: Perspective in Ethology, volume 3: Social Behavior. Springer, London.

Gil-Delgado JA. 1983. Breeding bird community in orange groves. In: Purroy FJ (ed.) Bird census and Mediterranean Landscape. Proceedings of the VII International Conference on Bird Census: 100-106. León: Universidad de León.

Gillis EA, Green DJ, Middleton HA and Morrissey CA. 2008. Life history correlates of alternative migratory strategies in American dippers. Ecology 89: 1687-1695.

Ginn HB and Melville DS. 1983. Moult in Birds. BTO guide nº 19. The British Trust for Ornithology, Beech Grove, Tring, Hertfordshire, England.

Gómez-Tejedor H and de Lope F. 1993. Sucesión fenológica de las aves no passeriformes en el vertedero de Badajoz. Ecología 7: 419-427.

Gómez-Tejedor H. 1998. Comportamiento Cleptoparásito del Milano Real Milvus milvus en un vertedero. In: Chancellor, R.D., B.-U. Meyburg & J.J. Ferrero (eds). Holarctic birds of prey: proceedings of an international conference: Actas del Congreso Internacional sobre Rapaces del Holártico: Bajadoz, Extremadura (Spain), 17-22 April 1995. Pp. 173-176. Asociación para la Defensa de la Naturaleza y los Recursos de Extremadura.

Gordo O and Doi H. 2012a. Drivers of population variability in phenological responses to climate change in Japanese birds. Climate Research 54: 95-112.

Gordo O and Doi H. 2012b. Spring phenology delays in an insular subtropical songbird: is response to climate change constrained by population size? Journal of Ornithology 153: 355-366.

Gordo O and Sanz JJ. 2005. Phenology and climate change: a long-term study in a Mediterranean locality. Oecologia 146: 484-495.

Gordo O and Sanz JJ. 2006. Climate change and bird phenology: a long-term study in the Iberian Peninsula. Global Change Biology 12: 1993-2004.

Gordo O and Sanz JJ. 2008. The relative importance of conditions in wintering and passage areas on spring arrival dates: the case of long-distance Iberian migrants. Journal of Ornithology 149: 199-210.

Gordo O, Brotons L, Ferrer X and Comas P. 2005. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? Global Change Biology 11: 12-21.

Gordo O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. Climate Research 35: 37-58.

Greenberg R. 1986. Competition in migrant birds in the nonbreeding season. Current Ornithology 3: 281-307.

Grieco F, van Noordwijk AJ and Visser ME. 2002. Evidence for the effect of learning on timing of reproduction in blue tits. Science 296: 136-138.

Guillemain M, Mondain-Monval JY, Johnson AR, and Simon G. 2005. Long-term climatic trend and body size variation in teal Anas crecca. Wildlife Biology 11(2): 81-88.

Guillemette M, Pelletier D, Grandbois JM and Butler PJ. 2007. Flightlessness and the energetic cost of wing molt in a large sea duck. Ecology 88(11): 2936-2945.

Gunnarsson G, Waldenström J and Fransson T. 2012. Direct and indirect effects of winter harshness on the survival of Mallards Anas platyrhynchos in northwest Europe. Ibis 154: 307–317.

Gwinner E and Neusser V. 1985. Die Jugendmauser afrikanischer Schwarzkehlchen (Saxicola rubicula und axillaries) sowie von F1-Hybriden. Journal of Ornithology 126: 219-220.

Hahn S, Bauer S and Liechti F. 2009. The natural link between Europe and Africa–2.1 billion birds on migration. Oikos. 118(4): 624-626.

Haley MP, Deutsch CJ and Le Boeuf BJ. 1994. Size, dominance and copulatory success in male northern elephant seals, Mirounga anguirostris. Animal Behaviour 48: 1249-1260.

Hall KSK and Tullberg BS. 2004. Phylogenetic analyses of the diversity of moult strategies in Sylvidae in relation to migration. Evolutionary Ecology 18: 85–105.

Handrinos G and Akriotis T. 1997. The birds of Greece. Christopher Helm Publishers Ltd. London.

Hannah L, Midgley GF and Millar D. 2002. Climate change-integrated conservation strategies. Global Ecology & Biogeography. 11: 485-495.

Harrison XA, Blount JD, Inger R, Norris DR and Bearhop S. 2011. Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80: 4–18.

Hawkins GL, Hill GE and Mercadante A. 2012. Delayed plumage maturation and delayed reproductive investment in birds. Biological reviews 87(2): 257-274.

Heath JA, Steenhof K and Foster MA. 2012. Shorter migration distances associated with higher winter temperatures suggest a mechanism for advancing nesting phenology of American kestrels Falco sparverius. Journal of Avian Biology 43: 376-384

Hedenstrom A, Barta Z, Helm B, Houston AI, McNamara JM and Jonzén N. 2007.Migration speed and scheduling of annual events by migrating birds in relation to climate change. Climate Research, 35: 79-91.IPCC 2007

Hedenström A. 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. Philosophical Transactions of the Royal Society of London Series B 363: 287–299.

Hedenström A and Sunada S. 1999. On the aerodynamics of moult gaps in birds. Journal of Eperimental Biology 202: 67-76.

Hedenström A, Barta Z, Helm B, Houston AI, McNamara JM and Jonzén N. 2007. Migration speed and scheduling of annual events by migrating birds in relation to climate change. Climate Research 35: 79-91.

Helm B and Gwinner E. 1999. Timing of postjuvenil molt in African Saxicola torquata axillaris and European Saxicola torquata rubicola Stonechats: effects of genetic and environmental factors. The Auk 116(3): 589-603.

Herremans M. 1991. Patterns in renewal of greater-coverts and timing of migration in juvenile Blackcaps Sylvia atricapilla in Belgium. Ringing & Migration, 12: 75-79.

Herrera CM. 1978. On the breeding distribution pattern of European migrant Birds: MacArthur's theme re-examined. The Auk 95: 496-509.

Hickling R, Roy DB, Hill JK, Fox R and Thomas CD. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12: 450-455.

Horion S, Cornet Y, Erpicum M and Tychon B. 2013. Studying interactions between climate variability and vegetation dynamic using a phenology based approach. International journal of applied earth observation and geoinformation. 20: 20-32.

Hötker H. 2002. Arrival of Pied Avocets Recurvirostra avosetta at the breeding site: effects of winter quarters and consequences for reproductive success. Ardea 90: 379-387.

Huberty CJ and Olejnik S. 2006. Applied MANOVA and Discriminant Analysis, Second Edition. Hoboken, New Jersey: John Wiley and Sons Inc.

Hulme M, Doherty R, Ngara T, New M, and Lister D. 2001. African climate change: 1900-2100. Climate Research 17: 145-168.

Hulme MF and Cresswell W. 2012. Density and behaviour of Whinchats Saxicola rubetra on African farmland suggest that winter habitat conditions do not limit European breeding populations. Ibis 154: 680-694.

Huntingford FA, Metcalfe NB, Thorpe JE, Graham WD and Adams CE. 1990. Social dominance and body size in Atlantic salmon parr Salmo salar L. Journal of Fish Biology 36: 877-881.

Huntley B, Green RE, CollinghamYC and Willis SG. 2007. A Climatic Atlas of European Breeding Birds. Barcelona: Lynx.

Hurvich CM and Chih-Ling T. 2008. A corrected Akaike Information Criterion for vector autoregressive model selection. Journal of Time Series Analysis 14: 271-279.

IPCC 2007: Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.)]. IPCC, Geneva, Switzerland, 104 pp.

Jaffré M, Beaugrand G, Goberville É, Jiguet F, Kjellén N, Troost G, Dubois PJ, Leprêtre A and Luckzac C. 2013. Long-Term Phenological Shifts in Raptor Migration and Climate. PLoS ONE 8(11): e79112.

Jahn AE, Levey DJ, Farias IP, Mamani AM, Vidoz JQ and Freeman B. 2010a. Morphological and genetic variation between migratory and non-migratory tropical Kingbirds during spring migration in central South America. The Wilson Journal of Ornithology 122(2): 236-243.

Jahn AE, Levey DJ, Hostetler J a, Mamani AM. 2010b. Determinants of partial bird migration in the Amazon Basin. The Journal of animal ecology 79: 983–992.

Jenni L and Winkler R. 1994. Moult and ageing of European passerines. Academic Press.

Jenni L and Kéry M. 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. Proceedings Royal Society of London B 270: 1467–1471.

Jenni L and Winkler R. 1994. Moult and ageing of European Passerines. Academic Press, London.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. Nature 491: 444-448.

Johnson DH. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology, 61, 65-71.

Jonzén N, Hedenström A and Lundberg P. 2007. Climate change and the optimal arrival of migratory birds. Proceedings of the Royal Society of London B 274: 269-274.

Jonzen N, Linden A, Ergon T, Knudsen E, Vik JO, Rubolini D, Piacentini D, Brinch C, Spina F, Karlsson L, Stervander M, Andersson A, Waldenstrom J, Lehikoinen A, Edvardsen E, Solvang R and Stenseth NC. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. Science 312: 1959-1961.

Jordano P and Herrera CM. 1981. The frugivorous diet of Blackcap populations Sylvia atricapilla wintering in southern Spain. Ibis 123: 502-507.

Jukema J and Hulscher JB. 1988. Recovery rate of ringed Golden Plovers Pluvialis apricaria in relation to the severity of the winter. Limosa 61: 85–90.

Kaiser A. 1993. A new multi-category classification of subcutaneous fat deposit of songbirds. Journal of Field Ornithology, 64(2): 246-255.

Kanamitsu M, Ebisuzaki W, Woollen J, Yang SK, Hnilo JJ, Fiorino M and Potter GL. 2002. NCEP-DOE AMIP-II Reanalysis (r-2). Bulletin of the American Meteorological Society 83: 1631-1644.

Karell P, Ahola K, Karstinen T, Valkama J and Brommer J 2011. Climate change drives microevolution in a wild bird. Nat Commun 2: 208

Kemp MU, van Loon EE, Shamoun-Baranes J and Bouten W. 2012. RNCEP: global weather and climate data at your fingertips. Methods in Ecology and Evolution 3: 65-70.

Ketterson ED and Nolan V Jr. 1983. The evolution of differential migration. Current Ornithology 1: 357-402.

Ketterson ED and Nolan V Jr. 1988. A possible role for experience in the regulation of the timing of bird migration. In: Ouellet H (ed) Proc XIX Int Ornithol Congr, Univ Ottawa Press, Ottawa, pp 2169–2179.

Kirschner M and Gerhart J. 1998. Evolvability. Proceedings of the National Academy of Science 95: 158420-158427.

Klaassen RH, Hake M, Strandberg R, Koks BJ, Trierweiler C, Exo KM, Bairlein F and Alerstam T. 2014. When and where does mortality occur in migratory birds? Direct evidences from long-term satellite tracking of raptors. Journal of Animal Ecology 83(1): 176-184.

Knudsen E, Lindén A, Both C, Jonzén N, Pulido F, Saino N, Sutherland W, Bach L, Coppack T, Ergon T, Gienapp P, Gill J, Gordo O, Hedenström A, Lehikoinen E, Marra P, Møller AP, Nilsson A, Péron G, Ranta E, Rubolini D, Sparks TH, Spina F, Studds C, Sæther S, Tryjanowski P and Stenseth NC. 2011. Challenging claims in the study of migratory birds and climate change. Biological Reviews 86: 928-946.

Kujala H, Vepsäläinen V, Zuckerberg B and Brommer JE. 2013. Range margin shifts of birds revisited – the role of spatiotemporally varying survey effort. Global Change Biology 19: 420-430.

La Sorte FA and Thompson FR. 2007. Poleward shifts in winter ranges of North American birds. Ecology 88: 1803-1812.

Laaksonen T, Ahola M, Eeva T, Risto AV and Lehikoinen E. 2006. Climate change, migratory connectivity and changes in laying date and clutch size of the pied flycatcher. Oikos 114: 277-290.

Larsson K. 1996. Genetic and environmental effects on the timing of wing moult in the barnacle goose. Heredity, 76: 100-107.

Leal A, Monrós JS and Barba E. 2004. Migration and wintering of Blackcaps Sylvia atricapilla in Eastern Spain. Ardeola 51(2): 345-355.

Lehikoinen A and Jaatinen K. 2012. Delayed autumn migration in northern European waterfowl. Journal of Ornithology 153: 563-570.

Lehikoinen A, Jaatinen K, Vähätalo AV, Clausen P, Crowe O, Deceuninck B, Hearn R, Holt C A, Hornman M, Keller V, Nilsson L, Langendoen T, Tománková I, Wahl J and Fox AD. 2013. Rapid climate driven shifts in wintering distributions of three common waterbird species. Global Change Biology 19(7): 2071-2081.

Lehikoinen E and Sparks TH. 2010. Changes in migration. In: Effects of climate change on birds (eds. A.P. Møller, W. Fiedler & P. Berthold), pp 89-112. Oxford: Oxford University Press.

Lehikoinen E, Sparks TH and Zalakevicius M. 2004. Arrival and departure dates. Advances in Ecological Research 35: 1-31.

Leisler B and Winkler H. 2003. Morphological consequences of migration in passerines. In: Bird migration (eds Berthold P, Gwinner E and Sonnenschein E), pp. 175–176. Berlin, Germany: Springer

Lemoine N and Böhning-Gaese K. 2003. Potential impact of global climate changes on species richness of long-distance migrants. Conservation Biology 17: 577-586.

Letcher T (ed.) 2009. Climate Change. Observed impacts on Planet Earth. Amsterdam: Elsevier.

Linderholm H.W. 2006. Growing season changes in the last century. Agricultural and Forest Meteorology, 137: 1–14.

Lindström A., Visser G.H. and Dann S. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. Physiological Zoology, 66: 490-510.

Lo Valvo F, Lo Verde G and Lo Valvo M. 1988. Relationships among wing length, wing shape and migration in Blackcap Sylvia atricapilla populations. Ringing & Migration 9(1): 51-54.

Lok T, Overdijk O, Piersma T. 2013. Migration Tendency Delays Distributional Response to Differential Survival Prospects along a Flyway. The American Naturalist 181(4): 520.

Lok T, Overdijk O, Tinbergen JM and Piersma T. 2011. The paradox of spoonbill migration: most birds travel to where survival rates are lowest. Animal Behaviour 82: 837–844.

Lundberg P. 1985. Dominance behaviour, body weight and fat variations, and partial migration in European blackbirds Turdus merula. Behavioral Ecology and Sociobiology 17(2): 185-189.

Maclean IMD, Austin GE, Rehfisch MM, Blew J, Crowe O, Delany S, Devos K, Deceuninck B, Günther K, Laursen K, Van Roomen M, Wahl J. 2008 Climate change causes rapid changes in the distribution and site abundance of birds in winter. Global Change Biology, 14: 2489–2500.

Máñez M, Tortosa FS, Barcell M and Garrido H. 1994. La invernada de la cigüeña blanca en el suroeste de España. Quercus 105: 10-12.

Marchamalo J, Blanco G and Prieto J. 1998. Presencia durante el otoño de la cigüeña blanca (Ciconia ciconia) en la Comunidad de Madrid (1991-1997). Anuario ornitológico de Madrid 1997: 14-21.

MARM 2009. Banco de datos de anillamiento de la Oficina de Especies Migratorias. Ministerio de Medio Ambiente, y Medio Rural y Marino. Madrid. [accessed: december 2009].

Marra PP. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. Behavioral Ecology 11(3): 299-308.

Martí R and del Moral JC (eds.) 2004. Atlas de las aves reproductoras de España. Parques Nacionales. Madrid, Spain. ISBN 978-84-8014-474-2

Martínez JE and Sánchez-Zapata JA. 1999. Wintering of booted eagles (Hieraaetus pennatus) and short-toed eagles (Circaetus gallicus) in Spain. Ardeola 46: 93–96.

Martins EP and Hansen TF. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. American Naturalist 149(4): 646-667.

Matthews SN, O'Connor RJ, Iverson LR and Prasad AM. 2004. Atlas of climate change effects in 150 bird species of the Eastern United States. General Technical Report NE-318. Delaware: USDA Forest Service.

Matthiesen DG. 1990. Avian medullary bone in the fossil record, an example from the Early Pleistocene of Olduvai Gorge, Tanzania. Journal of Vertebrate Paleontology 9: 34

Matthysen E. 1990. Non-breeding social organization in Parus. Current Ornithology 7: 209 -249.

McNamara JM and Houston AI. 2008. Optimal annual routines: behaviour in the ontext of physiology and ecology. Philosophical Transactions of the Royal Society of London B, 363: 301-319.

Mellone U, López-López P, Limiñana R and Urios V. 2012. Wintering habitats of Eleonora's Falcons Falco eleonorae in Madagascar. Bird Study 59: 29-36

Mellone U, Klaassen RH, García-Ripollés C, Limiñana R, López-López P, Pavón D, Strandberg R, Urios V, Vardakis M and Alerstam T. 2012. Interspecific comparison of the performance of soaring migrants in relation to morphology, meteorological conditions and migration strategies. PLoS ONE 7: 39833.

Mellone U, López- López P, Limiñana R, Piasevoli G and Urios V. 2013. The transequatorial loop migration system of Eleonora's falcon: differences in migration patterns between age classes, regions and seasons. Journal of Avian Biology: in press

Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, Alm-Küber K, Bissolli P, Braslavská O, Briede A, Chmielewski FM, Crepinsek Z, Curnel Y, Dahl Å, Defila C, Donnelly A, Filella I, Jatczak K, Måge F, Mestre A, Nordli Ø, Peñuelas J, Pirinen P, Remisová V, Scheifinger H, Striz M, Wielgolaski FE, Zach S and Zust A. 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12: 1969-1976.

Menzel A. and Fabian P. 1999. Growing season extended in Europe. Nature, 397: 659.

Merilä J, Kruuk LEB and Sheldon BC. 2001. Cryptic evolution in a wild bird population. Nature 412: 76-79.

Merilä J. 2012. Evolution in response to climate change: in pursuit of the missing evidence. Bioessays 34: 811-818.

Mezquida E, Villarán A and Pascual-Parra J. 2007. Timing of autumn bird migration in central Spain in light of recent climate change. Ardeola 54(2): 251-259.

Milá B, Smith TB and Wayne RK. 2006. Postglacial population expansion drives the evolution of long-distance migration in a songbird. Evolution 60: 2403–2409.

Milá B, Wayne RK, Smith TB. 2008. Ecomorphology of migratory and sedentary populations of the Yellow-Rumped warbler (Dendroica coronata). The Condor 110: 335–344.

Molina B and Del Moral JC. 2005. La cigüeña blanca en España. VI Censo internacional (2004). SEO/BirdLife. Madrid.

Møller AP, Fiedler W and Berthold P (eds.) 2004. Birds and Climate Change. Oxford: Academic Press.

Møller AP, Fiedler W, Berthold P (eds.) 2010. Effects of climate change on birds. Oxford: Oxford University Press.

Moller AP, Rubolini D and Lehikoinen E. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences USA 105: 16195-16200.

Mönkkönen M. 1995. Do migrant birds have more pointed wings? A comparative study. Evolutionary Ecology 9(5): 520-528.

Moreau RE. 1972. The Palearctic-African Bird migration Systems. Academic Press,London.

Morganti M and Pulido F. 2012. Invernada de migradores transaharianas en España. In: Palomino D, Bermejo A, Molina B, del Moral JC, editors. Atlas de las aves en invierno en España 2007-2010. Madrid: Ministerio de Agricultura, Alimentación y Medio Ambiente-SEO/BirdLIfe.

Morganti M, Mellone U, Bogliani G, Saino N, Ferri A, Spina F and Rubolini D. 2011. Flexible tuning of departure decisions in response to weather in Black redstart Phoenicurus ochruros migrating across the Mediterranean sea. Journal of Avian Biology 42: 323-334.

Morganti M. 2013. Male Blackcap singing from the nest. British Birds 106 (7): 415

Mueller T, O'Hara RB, Converse SJ, Uranek RP and Fagan WF. 2013. Social learning of migratory performance. Science 341(6149): 999-1002.

Mullen LM, Hoekstra HE. 2008. Natural Selection along an environmental gradient: a classic cline in mouse pigmentation. Evolution 62(7): 1555-1570.

Murphy ME. 1996. Energetics and nutrition of moult. In: Carey C (ed) Avian Energetics and Nutritional Ecology. Chapman & Hall, New York. pp 31–60.

Murphy ME and King JR. 1992. Energy and nutrient use during moult by White-crowned Sparrows Zonotrichia leucophrys gambelii. Ornis Scandinavica 23: 304-313.

Negro JJ, De la Riva M and Bustamante J. 1991. Patterns of winter distribution and abundance of Lesser Kestrels (Falco naumanni) in Spain. Journal of Raptor Research, 25: 30-35.

Neto JM, Gordinho L, Belda EJ, Marin M, Monrós J, Fearon P and Crates R. 2013. Phenotypic divergence among west European populations of Reed Bunting Emberiza schoeniclus: the effects of migratory and foraging behaviour. PLoS ONE 8(5): e63248.

Neumann C, Duboscq J, Dubuc C, Ginting A, Irwan AM, Agil M, Widdig A and Engelhardt A. 2011. Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. Animal Behaviour 82(4): 911-921.

Newton I and Dale LC. 1996a. Bird Migration at different latitudes in Eastern north America. The Auk 113(3): 626-635

Newton I and Dale LC. 1996b. Relationship between migration and latitude among west European birds. Journal of Animal Ecology 65(2): 137-146.

Newton I. 1998. Population limitation in birds. London: Academic Press.

Newton I. 2004. Population limitation in migrants. Ibis 146: 197-226

Newton I. 2008. The migration Ecology of birds. Academic Press, London.

Newton I. 2009. Moult and plumage. Ringing & Migration, 24: 220–226.

Nicholson SE. 2001. Climatic and environmental change in Africa during the last two centuries. Climate Research 17: 123-144.

Nilsson ALK, Lindstöm Å, Jonzén N, Nilsson SG and Karlsson L. 2006. The effect of climate change on partial migration: the blue tit paradox. Global Change Biology 12(10): 2014-2022.

Nilsson ALK, Nilsson JA, Alerstam T and Bäckman J. 2010. Migratory and resident blue tits Cyanistes caeruleus differ in their reaction to a novel object. Naturwissenschaften 97(11): 981-985.

Norman SC. 1990. A comparative study of post-juvenile moult in four species of Sylvia warbler. Ringing & Migration 11: 12-22.

Norris DR. 2005. Carry-over effects and habitat quality in migratory populations. Oikos 190: 178-186.

Noskov G.A., Rymkevich T.A. and Iovchenko N.P. 1999. Intraspecific variation of moult: Adaptive significance and ways of realisation. In: Adams N.J. and Slotow R.H. (eds): Proceedings of the 22nd International Ornithological Congress, Durban. BirdLife South Africa, Johannesburg. pp 544-563.

Ockendon N, Leech D, Pearce-Higgins JW. 2013. Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds. Biology letters 9: 20130669.

Onrubia A, Gómez J, Lobo L, Zufiaur F and Andrés T. 1996. Algunos apuntes sobre la Curruca Capirotada a partir de los datos de una Estación de Esfuerzo Constante en Alava. Apus 7-8: 19-23.

Palomino D, Bermejo A, Molina B and Del Moral J (eds.). 2012. Atlas de las aves en invierno en España 2007-2010, Ministerio de Agricultura, Alimentación y Medio Ambiente-SEO/BirdLife, Madrid, Spain.

Palomino D. 2006. El milano negro en España. I Censo Nacional (2005). SEO/BirdLife. Madrid.

Pan W. 2001. Akaike's Information Criterion in Generalized Estimating Equations. Biostatitics 57(1): 120-125.

Paradis E, Claude J and Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20: 289-290.

Parmesan C and Yohe G. 2003. A globally coherent fingerprint of climate impacts across natural systems. Nature 421: 37-42.

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA and Warren M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399: 579-583

Parmesan C. 2006. Ecological and evolutionary response to recent climate change. Annual Review of Ecology, Evolution and Systematics 37: 637-669.

Pausas JG. 2004. Changes in fire and climate in the Eastern Iberian Peninsula (Mediterranean Basin). Climatic Change 63: 337–350.

Pautasso M. 2012. Observed impacts of climate change on terrestrial birds in Europe: an overview. Italian Journal of Zoology 79: 296-314.

Pearce-Higgins JW, Yalden DW, Dougall TW and Beale CM. 2009. Does climate change explain the decline of a trans-Saharan Afro-Palaearctic migrant?. Oecologia 159: 649-659.

Pérez-Tris J and Tellería JL. 2001. Age-related variation in wing morphology of migratory and sedentary blackcaps, Sylvia atricapilla. Journal of Avian Biology 32: 207-21

Pérez-Tris J and Tellería JL. 2002. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. Journal of Animal Ecology 71: 211–224

Pérez-Tris J, Bensch S, Carbonell R, Helbig AJ and Tellería JL. 2004. Historical diversification of migration patterns in a passerine bird. Evolution 58: 1819–1832.

Pérez-Tris J, Carbonell R and Tellería JL. 1999. A method for differentiating between sedentary and migratory Blackcaps. Bird Study 46: 299–304.

Pinheiro J, Bates D, DebRoy S, Sarkar D and the R Development Core Team. 2012. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-105.

Plomin R. 1990. The role of inheritance in behaviour. Science 248: 183-188.

Pulido F and Berthold P. 2004 Microevolutionary response to climatic change. Advances in Ecological Research 35: 151-183.

Pulido F and Berthold P. 2010. Current Selection for lower migratory activity will drive the evolution of residency in a migratory bird population. PNAS 107: 7341-7346.

Pulido F and Widmer M. 2005. Are long-distance migrants constrained in their evolutionary response to environmental change? Annals of the New York Academy of Science 1046: 228-241.

Pulido F, Berthold P and van Noordwijk AJ. 1996. Frequency of migrants and migratory activity are genetically correlated in a bird population: evolutionary implications. Proceedings of the National Academy of Science USA 93: 14642 – 14647.

Pulido F, Berthold P, Mohr G and Querner U. 2001. Heritability of the timing of autumn migration in a natural bird population. Proceedings of the Royal Society of London B 268: 953-959.

Pulido F, Berthold P. 2010. Current Selection for lower migratory activity will drive the evolution of residency in a migratory bird population. Proceedings of the National Academy of Sciences 107: 7341-7346.

Pulido F, van Noordwijk AJ and Berthold P and 1996. Frequency of migrants and migratory activity are genetically correlated in a bird population:

evolutionary implications. Proceedings of the National Academy of Science USA 93: 14642 – 14647.

Pulido F. 2007a. Phenotypic changes in spring arrival: evolution, phenotypic plasticity, effects of weather and condition. Climate Research 35: 5-23.

Pulido F. 2007b. The Genetics and Evolution of Avian Migration. BioScience 57: 165-174.

Pulido F. 2011. Evolutionary genetics of partial migration - the threshold model of migration revis(it)ed. Oikos 120: 1776–1783.

Pulido F. and Berthold P. 2003. Quantitative genetic analysis of avian behaviour. In: Berthold P., Gwinner E. and Sonnenschein E. (eds): Avian Migration. Springer-Verlag, Berlin. pp 53-77.

Pulido F. and Berthold P. 2010. Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. Proceedings of the National Academy of Science, 107: 7341-7364.

Pulido F. and Coppack T. 2004. Correlation between timing of juvenile moult and onset of migration in the blackcap Sylvia atricapilla. Animal Behaviour, 68(1): 167-173.

Rappole JH and Tipton AR. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62: 335-337.

Rey PJ. 1993. The role of olive orchards in the wintering of frugivorous birds in Spain. Ardea 81: 151-160.

Rey PJ. 1995. Spatio-temporal variation in fruit and frugivorous bird abundance in olive orchards. Ecology 76: 1625-1635.

Rey PJ. 2011. Preserving frugivorous birds in agro-ecosystems: lessons from Spanish olive orchards. Journal of Applied Ecology 48: 228-237.

Robb GN, McDonald RA, Chamberlain DE and Bearhop S. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian population. Frontiers in Ecology and the Environment, 6: 476-484.

Robinson RA, Crick HQP, Learmonth JA, Maclean IMD, Thomas CD, Bairlein F, Forchhammer MC, Francis CM, Gill JA, Godley BJ, Harwood J, Hays GC, Huntley B, Hutson AM, Pierce GJ, Rehfisch MM, Sims DW, Santos BM, Sparks TH, Stroud DA and Visser ME. 2009. Travelling through a warming world: climate change and migratory species. Endangered Species Research 7: 87-99.

Robson D and Barriocanal C. 2011. Ecological conditions in wintering and passage areas as determinants of timing of spring migration in trans-Saharan migratory birds. Journal of Animal Ecology 80: 320–331.

Rodgers AR, Carr AP, Beyer HL, Smith L and Kie JG. 2007. HRT: Home Range Tools for ArcGIS. Version 1.1. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Roff D.A. 2002. Life history Evolution. Sinauer, Sunderland, Massachusetts.

Rohwer VG, Rohwer S and Ramirez MFO. 2009. Molt biology of resident and migrant birds of the monsoon region of West Mexico. Ornitología Neotropical 20(4): 565-584.

Rolshausen G, Hobson KA and Schaefer HM. 2010. Spring arrival along a migratory divide of sympatric Blackcaps (Sylvia atricapilla). Oecologia 162: 175-183.

Rolshausen G, Segelbacher G, Hobson KA and Schaefer HM. 2009 Contemporary Evolution of Reproductive Isolation and Phenotypic Divergence in Sympatry along a Migratory Divide. Current Biology 19(24): 2097-2101.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C and Pounds JA. 2003. Fingerprints of global warming on wild animals and plants. Nature 421: 57-60.

Royle NJ, Lindström J and Metcalfe NB. 2005. A poor start in life negatively affects dominance status in adulthood independent of body size in green swordtails Xiphophorus helleri. Proc Roy Soc London B 272(1575): 1917-1922.

Rubolini D, Møller AP, Rainio K and Lehikoinen E. 2007. Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. Climate Research 35: 135-146.

Rubolini D, Saino, N and Møller AP. 2010. Migratory behaviour constrains the phenological response of birds to climate change. Climate Research 42: 45-55.

Rutte C, Taborsky M, Brinkhof MWG. 2006. What sets the odds of winning and losing? Trends in ecology & evolution 21: 16–21.

Saino N, Ambrosini R, Rubolini D, Von Hardenberg J, Provenzale A, Huppop K, Huppop O, Lehikoinen A, Lehikoinen E, Rainio K, Romano M and Sokolov L. 2011. Climate warming, ecological mismatch at arrival and population decline in migratory birds. Proceedings of the Royal Society of London B 278: 835-842.

Saino N, Rubolini D, von Hardenberg J, Ambrosini R, Provenzale A, Romano M and Spina F. 2010. Spring migration decisions in relation to weather are predicted by wing morphology among trans-Mediterranean migratory birds. Functional Ecology 24: 658–669.

Saino N, Szép T, Ambrosini R, Romano M and Møller AP. 2004. Ecological conditions during winter affect sexual selection and breeding in a migratory bird. Proceedings of the Royal Society of London B 271: 681-686

Saino N, Szép T, Romano M, Rubolini D, Spina F and Møller AP. 2004. Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. Ecology Letters 7: 21–25.

Salewski V and Bruderer B. 2007. The evolution of bird migration. A synthesis. Naturwissenschaften 94: 268-279.

Sanz-Aguilar A, Béchet A, Germain C, Johnson AR and Pradel R. 2012. To leave or not to leave: survival trade-offs between different migratory strategies in the greater flamingo. Journal of Animal Ecology 81: 1171-1182.

Schabenberger O and Pierce FJ. 2002. Contemporary Statistical Models for the Plant and Soil Sciences. New York: CRC Press.

Schieltz PC and Murphy ME. 1997. The contribution of insulation changes to the energy cost of avian molt. Canadian Journal of Zoology 75: 396-400.

Senar JC and Borrás AB. 2004. Sobrevivir al invierno: estrategias de las aves invernantes en la Península Ibérica. Ardeola 51: 133–168.

SEO/BirdLife 2012a. Atlas de las aves en invierno en España 2007-2010. Ministerio de Agricultura, Alimentación y Medio Ambiente-SEO/BirdLife. Madrid, Spain.

SEO/BirdLife 2012b. Análisis preliminar del banco de datos de anillamiento de aves del Ministerio de Agricultura, Alimentación y Medio Ambiente, para la realización de un atlas de migración de aves de España. SEO/BirdLife-Fundación Biodiversidad. Madrid.

SEO/Birdlife. 2013. Enciclopedia virtual de las aves de España www.enciclopediadelasaves.org Sociedad Española de Ornitología, Madrid. Accessed: 10-01-2013

Shaffer SA, Tremblay Y, Weimerskirch H, Scott D, Thompson DR, Sagar PM, Moller H, Taylor GA, Foley DG, Block BA, Costa DP 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. Proceedings of the National Academy of Sciences USA 103: 12799-12802.

Sheldon FH, Whittingham LA, Moyle RG, Slikas B and Winkler DW. 2005. Phylogeny of swallows (Aves: Hirundinidae) estimated from nuclear and mitochondrial DNA sequences. Molecular Phylogeny and Evolution 35: 254-270.

Shirihai H, Gargallo G and Helbig AJ. 2001. Sylvia Warblers. Princeton University Press. Princeton. New Jersey.

Siriwardena GM and Wernham CV. 2002. Synthesis of the migration patterns of British and Irish birds. In: Wernham CV, Toms MP, Marchant JH, Clark JA, Siriwardena GM, Baillie SR, editors. The Migration Atlas: Movements of Birds of Britain and Ireland. London: T. & A.D. Poyser. p. 70–102.

Smallegange IM, Fiedler W, Köppen U, Geiter O and Bairlein F. 2010. Tits on the move: exploring the impact of environmental change on blue tit and great tit migration distance. Journal of Animal Ecology 79: 350-357.

Snell-Rood EC and Cristol DA. 2005. Prior residence influences contest outcome in flocks of non-breeding birds. Ethology 111(5): 441-454.

Spina F and Volponi S. 2008. Atlante della migrazione degli uccelli in Italia. 2. Passeriformi. MATTM/ISPRA. Roma.

Sutherland WJ. 1998. Evidence for flexibility and constraint in migration systems. Journal of Avian Biology 29: 441-446.

Svensson E and Hedenström A. 1999. A phylogenetic analysis of the evolution of moult strategies in Western Palearctic warblers (Aves: Sylvidae). Biological Journal of the Linnean Society 67: 263-276.

Svensson L. 1992. Identification guide to European Passerines. 4th edition. Privately Published, Stockholm.

Swaddle JP and Witter MS. 1997. The effects of moult on the flight performance, body mass, and behaviour of European starlings Sturnus vulgaris: an experimental approach. Canadian Journal of Zoology 75: 1135-1146.

Szép T, Møller AP, Piper S, Nuttal R, Szabo ZD and Pap PL. 2006. Searching for potential wintering and migrationareas of a Danish barn swallow population in South Africa by correlating NDVI with survival estimates. J Ornithol 147: 245-253.

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, and Kumar S. 2011. MEGA 5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods 28: 2731-2739.

Taylor CM and Norris DR. 2007. Predicting conditions for migration: effects of density dependence and habitat quality. Biology Letters 3 280-284.

Tellería JL. 1981. La migración de las Aves en el Estrecho de Gibraltar. Vol. 2, Aves No Planeadoras. Madrid: Universidad Complutense de Madrid.

Tellería JL and Carbonell R. 1999. Morphometric variation of five Iberian blackcap Sylvia atricapilla populations. Journal of Avian Biology 30: 63-71.

Telleria JL and Pérez-Tris J. 2007. Habitat effects on resource tracking ability: do wintering Blackcaps Sylvia atricapilla track fruit availability? Ibis 149: 18-25.

Tellería JL, Blázquez M, de la Hera I and Pérez-Tris J. 2013. Migratory and resident Blackcap Sylvia atricapilla wintering in southern Spain show no resource partitioning. Ibis 155(4): 750-761.

Tellería JL, Ramírez A and Pérez-Tris J. 2005. Conservation of seed-dispersing migrant birds in Mediterranean habitats: shedding light on patterns to preserve processes. Biological Conservation 124: 493–502.

Tellería JL, Ramírez A and Pérez-Tris J. 2008. Fruit tracking between sites and years by birds in Mediterranean wintering grounds. Ecography 31: 381-388.

Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, Botham MS, Brereton TM, Bright PW, Carvalho L, Clutton-Brock T, Dawson A, Edwards M, Elliott JM, Harrington R, Johns D, Jones ID, Jones JT, Leech DI, Roy DB, Scott WA, Smith M, Smithers RJ, Winfield IJ and Wanless S. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Global Change Biology 16: 3304-3313.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Ferreira de Siqueira M, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Townsend-Peterson A, Phillips OL and Williams SE. 2004. Extinction risk from climate change. Nature 427: 145.

Thorup K, Tøttrup AP and Rahbek C. 2007. Patterns of phenological changes in migratory birds. Oecologia 151: 697-703.

Thorup K. 2006. Does the migration programme constrain dispersal and range size of migratory birds? 33: 1166-1171.

Tobias J. 1997. Asymmetric territorial contests in the European robin: the role of settlement costs. Animal Behaviour 54(1): 9-21.

Tokarz RR. 1985. Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (Anolis sagrei). Animal Behaviour 33(3): 746-753.

Tortosa FS, Caballero JM, and Reyes-López J. 2002. Effect of rubbish dumps on breeding success in the White Stork in southern Spain. Waterbirds 25: 39-43.

Tøttrup AP, Klaassen RHG, Kristensen MW, Strandberg R, Vardanis Y, Lindström Å, Rahbek C, Alerstam T and Thorup K. 2012. Drought in Africa caused delayed arrival of European songbirds. Science 338: 1307.

Tøttrup AP, Thorup K, Rainio K, Yosef R, Lehikoinen E and Rahbek C. 2008. Avian migrants adjust migration in response to enviromental conditions en route. Biology Letters. 4: 685-688.

Trierweiler C, Mullié WC, Drent RH, Exo KM, Komdeur J, Bairlein F, Harouna A, de Bakker M and Koks BJ. 2013. A Palaearctic migratory raptor species tracks shifting prey availability within its wintering range in the Sahel. Journal of Animal Ecology 82: 107-120.

Tryjanowski P, Kuźniak S and Sparks TH. 2005. What affects the magnitude of change in first arrival dates of migrant birds? Journal of Ornithology 146: 200-205.

Tucker CJ and Nicholson SE. 1999. Variation in the size of Sahara desert from 1980 to 1997. Ambio 28(7): 587-591.

Turner RK, van de Bergh JCJM, Söderqvist T, Barendregt A, van der Straaten J, Matlby E and vn Ierland EC. 2000. Ecological-economic analysis of wetlands: scientific integration for management and policy. Ecological Economics 35: 7-23.

Valiela I and Bowen JL. 2003. Shifts in winter distribution in birds: effects of global warming and local habitat change. Ambio 32: 476-480.

van Vliet J, Musters CJM and Ter Keurs WJ. 2009. Changes in migration behaviour of Blackbirds Turdus merula from the Netherlands. Bird Study 56: 276-281.

Végvári Z, BóKony V, Barta Z and Kovács G. 2010. Life history predicts advancement of avian spring migration in response to climate change. Global Change Biology 16: 1–11.

Vergara P and Fargallo JA. 2007. Delayed plumage maturation in Eurasian kestrels: female mimicry, subordination signalling or both? Animal Behaviour 74(5): 1505-1513.

Vickery JA, Ewing SR, Smith KW, Pain DJ, Bairlein F, Skorpilova J and Gregory RD. 2014. The decline of Afro-Palaearctic migrants and an assessment of potential causes. Ibis 156: 1-22.

Visser ME, Perdeck AC, van Balen JH and Both C. 2009. Climate change leads to decreasing bird migration distances. Global Change Biology 15: 1859–1865.

Visser ME. 2008. Keeping up with a warming world: assessing the rate of adaptation to climate change. Proceedings of the Royal Society of London B 275: 649-659.

Willi Y, Van Buskirk JV and Hoffmann AA. 2006. Limits to the adaptive potential of small populations. Annual Review of Ecology, Evolution, and Systematics 37: 433-458.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA and Smith GM. 2009. Mixed Effects Models and Extensions in Ecology with R. Statistics for Biology and Health. LaVergne: Springer.

Zwarts L, Bijlsma RG, van der Kamp J and Wymenga E. 2009. Living on the edge: wetland and birds in a changing Sahel. Zeist: KNNV Publishing.

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Section one: Shortening of migration distance in European trans-Saharan migrants

Chapter I. Wintering of trans-Saharan birds in Spain.

Chapter II. Recent establishment of European long-distance migratory bird species north of the Sahara in winter.

Chapter III. Shortening of migration distances in birds is not explained by recent climate warming.

Chapter IV. Rapid northward spread of recently established wintering populations of trans-Saharan birds in the Western Mediterranean.

Section two: Insights from a partial-migratory system in Eastern Spain

Chapter V. Complete post-juvenile moult in first-year Blackcaps: proximate causes and adaptive implications.

Chapter VI. Discrimination of residents and migrants by morphology and stable isotopes in a partially migratory Blackcap population.

Chapter VII. Habitat selection and social dominance in sympatric wintering and resident birds: adaptive consequences for partial-migration.